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Estimating the Energy Budgets of Actively Predatory Fishes[1]

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KERR, S. R. 1982. Estimating the energy budgets of actively predatory fishes. Can. J. Fish. Aquat. Sci. 39: 371–379.

Where estimates of surplus energy accumulation are available, bioenergetic analysis of fish in nature requires estimates of the associated ration or metabolic levels. The estimation procedure described here is based upon direct coupling of ration intake with the activity metabolism subcomponent of total metabolism. Its primary advantage over other estimation procedures is in its simple, generalized handling of activity metabolism. Application of the method is illustrated for natural populations of cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*.

Key words: bioenergetics, growth, metabolism, rations, cod, haddock

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Dans les cas où l'on dispose d'estimations de l'accumulation de surplus énergétiques, l'analyse bioénergétique des poissons dans la nature requiert des estimations de la ration ou des niveaux métaboliques qui leur sont associés. La méthode d'estimation décrite dans l'article qui suit est fondée sur l'association directe de l'ingestion de ration avec la sous-composante métabolisme d'activité du métabolisme total. Le principal avantage de cette méthode d'estimation réside dans la manipulation généralisée et simple du métabolisme d'activité. Nous illustrons son application à l'aide de populations naturelles de morues, *Gadus morhua*, et d'églefins, *Melanogrammus aeglefinus*.

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BIOENERGETIC analysis of fish production ultimately depends upon estimates of three primary variables. These are ration intake, R, metabolic dissipation, T, and the surplus energy increment, Δw (the portion of R retained as somatic and reproductive tissue), all measured in common units of energy over common intervals of time. A great strength of the bioenergetic approach is that each primary variable is, in principle, directly observable. In practice, however, field estimates of two of the three primary variables are laborious and expensive to obtain with established techniques, and seldom attain satisfactory levels of precision and accuracy.

Methods of growth determination for wild populations have been extensively investigated, and useful estimates can often be prepared with no more than "ordinary" difficulty (e.g. Ricker 1979). Unfortunately, conventional collection of growth data is usually restricted to length or, less often, weight increments; rarely are these accompanied by the energy conversion and gonad measurements necessary for unequivocal determination of surplus energy, Δw. This failure is procedural, however, and does not reflect any technical constraint; Δw is ordinarily measurable with straightforward procedures.

Reliable estimation of the remaining primary variables, T and R, is not so straightforward. In brief, field estimates of T have been based on the use of assumed constancy (e.g. the Winberg rule; Mann 1978) or various metabolic indicators (e.g. Edwards 1968), or derived through consideration of foraging costs (e.g. Ware 1975; Kerr 1971c). Similarly, estimates of R are based on some combination of techniques involving stomach analysis and clearance rates; sometimes an indicator or tracer is used: see Mann (1978) for a general review, and Elliot and Persson (1978) and Nakashima and Leggett (1978) for specific examples. It is no criticism of any of the foregoing examples to say that the relatively large number of assumptions and parameter estimates associated with each procedure combine to enhance the opportunities for increased uncertainty and variability of the ensuing estimates. Clearly, the possibility of any simpler procedure for estimating R or T is worth pursuing.

If we assume that Δw estimates are available, then the problem is essentially that of solving a single equation with two unknown variables. My aim is to develop an easy procedure for estimating either R or T for a given Δw. The approach offered here is based on both inferential and emperical evidence of a regular pattern of association between T and R. In what follows, I sketch the bioenergetic context of the problem, derive an approach to its solution, and test the approach with published data for a species of major commercial importance, the Atlantic cod, *Gadus morhua*. In principle the method, if confirmed, should be applicable to many actively predatory fish species, a prospect with considerable potential.

Relations of the Primary Variables

The basic bioenergetic equation used here is in the form set out by Winberg (1956)

$$(1) \quad pR = T + \Delta w$$

where the dimensionless coefficient p corrects for nonassimilation of rations, and the remaining variables are as defined above.

It is widely assumed that the metabolic component T can be meaningfully disaggregated. Thus, following Kerr (1971b)

$$(2) \quad T = T_s + T_c + T_F$$

where T_s is the standard (maintenance) metabolism (Fry 1947), T_c is the calorigenic metabolism or "SDA," specific to the utilization of food (Kleiber 1961), and T_F is the metabolic component associated with external activities. The activities potentially contributing to T_F can vary, particularly between laboratory and natural environments. These differences will be considered below.

The standard metabolism, T_s of equation (2), is a relatively well-investigated function of body size and exogenous variables such as temperature and salinity (Fry 1971). It is generally accepted that laboratory measures of T_s, determined either by respirometry or feeding experiments, are equally applicable to natural populations. For estimation of T_s, I use here the familiar power function

$$(3) \quad T_s = \alpha_s W^{\gamma}$$

where W is body weight and α_s and γ are fitted coefficients.

As with T_s, it appears that laboratory estimates of T_c can be validly extended to field conditions, with appropriate attention to diet type. In many cases, T_c is directly proportional to the ration, R (Kleiber 1961), i.e.

$$(4) \quad T_c = mR$$

Evidence for constancy of the coefficient m for various fishes has been provided by Beamish (1974), Kerr (1971a), Muir and Niimi (1972), and Ware (1975), among others, although Tandler and Beamish (1979) point to possible complications.

Substituting equation (2) into equation (1) gives

$$pR = T_s + T_F + T_c + \Delta w$$

and substituting for T_c from equation (4) gives

$$(p - m)R = T_s + T_F + \Delta w$$

Following Ware (1975) I define $\tau = p - m$, and then the basic equation for net energy takes the form

$$(5) \quad \tau R = T_s + T_F + \Delta w$$

As outlined above, τ and T_s can be determined from laboratory investigation. If Δw is directly observed, the problem becomes one of determining R or T_F. For this purpose, it is useful to examine the biokinetic limits of each variable in equation (5).

The total metabolism T is itself constrained to a maximum sustained aerobic limit T_T (Fry 1947), which can be set out in the form of equation (3).

$$(6) \quad T_T = \alpha_T W^{\gamma}$$

where the maximum level α_T, determined by conventional laboratory procedures, is in the order of 4.5 times the standard level T_s for cod (Edwards et al. 1972). The use of a constant slope γ in equations (3) and (6) may not be exactly correct (e.g. Brett and Groves 1979), but it is a convenient approximation to use, and does not affect the conclusions to follow. The primary advantage of constant γ is that it simplifies expression of all variables as multiples of T_s in the accompanying Fig. 1–3. In the numerical examples below, tem-

TABLE 1. Parameter values applied to numerical estimates for cod, together with sources and supplementary comments.

Parameter	Usage	Source/comments
$p = 0.98$ (lab) $p = 0.9$ (field)	Assimilation coefficient (dimensionless); see equation (1)	Rounded down somewhat from Edwards et al. (1972); field value rounded down to more realistic level for natural populations; see text discussion
$m = 0.15$	Calorigenic coefficient (dimensionless); see equation (4)	Rounded to nearest 0.05 from Ware (1975); see additional text references
$\alpha_s = 0.024$ (lab) $\alpha_s = 4.6$ (field)	Intercept of standard metabolism–body weight relationship; see equation (3); lab value expressed for metabolism in kcal·d^{-1} (4.184 × 10^3 J·d^{-1}) at 16°C; field value in kcal·yr^{-1} at 8°C	Composite value based upon Edwards et al. (1972), Jones and Hislop (1978), Kohler (1964), Saunders (1963); temperature conversion following Jones (1978)
$\gamma = 0.82$	Power index of metabolism–body weight relationship; see equations (3) and (6)	As for α_s above
$R_M = 6.0$ (lab) $R_M = 6.5$ (field)	Maximum ration (multiples of standard metabolism)	Lab value is average of "excess" ration levels from Edwards et al. (1972); field value adjusted for reason discussed in text
$T_T = 4.5$	Maximum metabolic rate (multiples of standard metabolism)	Average of highest rates from Edwards et al. (1972)

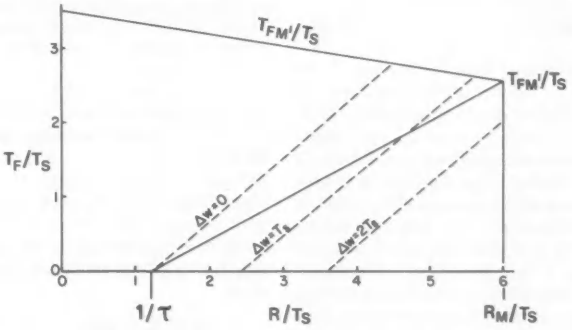

FIG. 1. Potential region for relationship between activity metabolism, T_F, and ration, R (both expressed as multiples of standard metabolism, T_s). For nonnegative growth (surplus energy accumulation), T_F and R are constrained to the zone to the right of the zero growth isopleth. The solid line $1/\tau = T_{FM}'/T_s$, showing the probable relationship, is mapped from Fig. 2. See text for further explanation.

perature corrections for both equations (3) and (6) have been made with the exponential method described by Jones (1978).

Given a metabolic limit T_T, it follows from equations (2) and (4) that there is potentially a maximum $T_F = T_{FM}$, given by

$$T_{FM} = T_T - T_s - mR \quad (7)$$

where T_{FM} is the maximum activity expenditure that could potentially be sustained at a given ration level. It also follows from equation (7) that there is an ultimate potential limit, T_{FM}', reached when $R = R_M$ (defined below), in equation (7).

There is evidence for an upper limit R_M to the ration level that can be sustained, and various procedures have been proposed for its estimation (Elliot 1975; Kitchell et al. 1977). For present purposes, the method of estimation used for R_M is unimportant, given the empirical observations of its existence and apparent predictability. What is important in the present context is that it appears to be relatively stable for given conditions of food type, body size, and ambient temperature.

The foregoing considerations can be conveniently summarized. Using numerical values appropriate to laboratory cod for m, R_M, p, T_T, and T_s from Table 1, the potential zone of T_F values relative to R is shown in Fig. 1, where T_{FM} has been estimated from equation (7). Although the figure is specific to cod, its general appearance, scaled in units of T_s, would be similar for most species of fish that forage actively. In brief, the figure shows that as R increases toward R_M, the potential latitude for activity metabolism T_{FM} decreases to the limit T_{FM}', because of the increasing calorigenic load, T_c. Also shown on the figure are some integer isopleths for Δw, calculated from equation (5). It should be noted that all variables are expressed as average, not instantaneous, values. Clearly, for an observed Δw, any combination of T_F and R which lies on the appropriate isopleth is possible. The remaining problem, accordingly, is to determine the actual combination of T_F and R realized on average by fish with an observed rate of surplus energy accumulation.

Activity Metabolism and Rations

A priori, it is important to consider some differences between activity metabolism expended in laboratory and natural environments (Kerr 1971a). In the wild, activity metabolism supports a variety of essential external activities, including foraging for prey, migration, reproductive behavior, and other behavioral interactions. Over relatively lengthy time periods, in the order of a year, it is likely that foraging costs will typically comprise the major portion of average activity metabolism. That is, I assume that T_F may be approximately equivalent to foraging metabolism, on average, for wild fishes, although other activity costs cannot be forgotten. Conversely, foraging costs are likely to comprise a minor portion of average activity metabolism in the bounded environment of most laboratory protocols, where the experimenter provides forage at some arbitrary level. Consequently, laboratory T_F often comprises mainly "spontaneous" (apparently undirected) activities (Fisher and Sullivan 1958), not importantly associated with foraging. Bearing this distinction between laboratory and natural environments in mind, I now examine the association of T_F with R in both environments.

Laboratory Environments

It is established that the level of total metabolism, T, increases regularly with the laboratory feeding level, R (Paloheimo and Dickie 1966a; Brett and Groves 1979; Huisman 1976; Edwards et al. 1972). Because T_s is constant for a given body size and ambient conditions, and because T_c is a constant fraction of R, it follows from equation (2) that the laboratory T_F also follows a regular pattern. This effect is shown for cod in Fig. 2, calculated from data provided by Edwards et al. (1972). Clearly, the data follow a linear pattern. Apart from these explicit examples, such regular patterns of association between activity metabolism and ration level are apparently common in laboratory experiments; Kerr (1971a) concluded that their existence is reflected in the ubiquitous growth efficiency regularities ("K-lines") described by Paloheimo and Dickie (1966b).

Inspection of Fig. 2 indicates an R intercept at $R = T_s/\tau$, corresponding (equation (5)) to a condition of zero activity at zero growth. Although one would expect some small level of foraging activity to be necessary for ration levels less than maintanance, the tendency for some species of fish to restrict activity severely at maintenance feeding has long been known (Brown 1957). Consequently, it is reasonable to use this intercept for description of the data.

The simplest assumption for Fig. 2 is a linear pattern, and the most direct description of a linear relationship passing through the observed R-intercept and the point R_M, T_{FM}' is

$$(8) \quad \frac{T_F}{R - T_s/\tau} = \frac{T_{FM}'}{R_M - T_s/\tau} \qquad R \geq T_s/\tau$$

where the restriction that R must equal or exceed maintenance ration recognizes that negative T_F would otherwise occur. From equation (7), recall that

$$T_{FM}' = T_T - T_s - mR_M$$

and from equation (5) that

$$T_F = \tau R - \Delta w - T_s$$

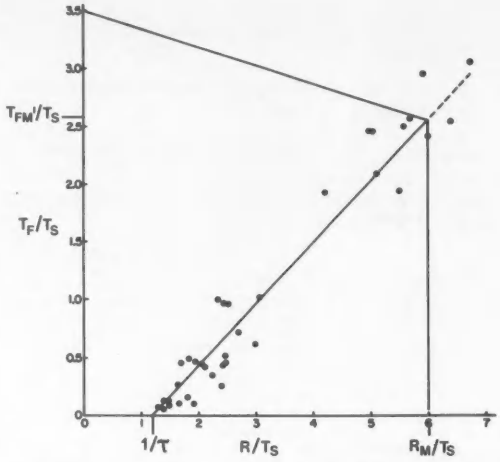

FIG. 2. Relation between T_F and R, calculated from data provided by Edwards et al. (1972). Units as in Fig. 1, but vertical scale expanded for better resolution of data. The fitted, solid line is described by equation (8), using parameters set out in Table 1.

Substituting these values for T_F and T_{FM}' in equation (8), and simplifying, making use of the definition $\tau = p - m$, leads to the form

$$(9) \quad \tau R = \frac{(\tau R_M - T_s)\Delta w}{pR_M - T_T} + T_s$$

for $R \geq T_s/\tau$. It should be noted that imposition of linearity on equation (8) has resulted in equation (9) having the general form

$$\tau R = T_s + a\Delta w$$

which differs from the form of equation (5). Note too that by reference to the definitions of Δw_M (see below) and T_{FM}', the constant term a can be equivalently written as

$$a = \frac{\Delta w_M + T_{FM}'}{\Delta w_M}$$

Using numerical values from Table 1, and data for Δw from Edwards et al. (1972), equation (9) can be used to estimate the ration level associated with a given Δw. As shown by the fitted line in Fig. 3, equation (9) clearly provides an adequate description of cod growth in the laboratory. In this instance, gonad production was apparently not a significant factor, and surplus energy, Δw, is equivalent to observed somatic growth.

Although equation (9) is simply a mathematical description, it is worth considering how the laboratory cod could regulate their activities in such a way as to be described by equation (9). Equation (8), from which equation (9) derives, implies that a fish is able to sense in some way its ration and activity levels relative to their respective maxima, R_M and T_{FM}'. There is ample evidence (Paloheimo and Dickie 1966a) that fishes possess suitable mechanisms for "comparing" some current level of R with R_M, but it is difficult to think of

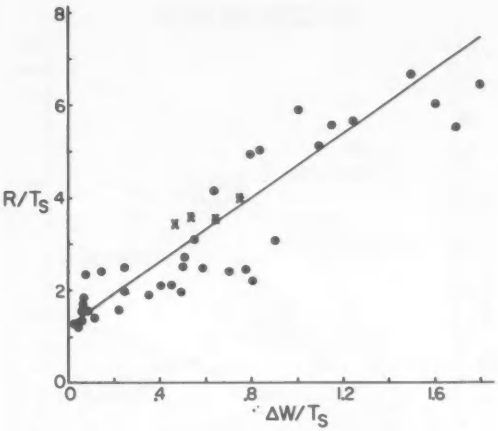

FIG. 3. Observed relation between cod ration and growth from Edwards et al. (1972) (closed circles, negative values omitted), compared with estimate from equation (9) (solid line). Crosses represent four additional averages from Kohler (1964). Energy conversions for Kohler's data followed Jones (1978).

a comparable signal by which a fish could sense T_{FM}' at any R level other than R_M.

It is more likely that a fish is able to sense its current total metabolism T (by cues such as blood gas tension, ventilation rate, or the like) relative to its maximum level T_T. This suggests that equation (8) could be recast in terms of total metabolism. In this case, for $R = T_s/\tau$, the corresponding T for maintenance rations now is $T_s + mT_s/\tau$, which includes both T_s and T_c. At R_M, metabolism is now T_T. With these changes we can write,

$$\frac{T - (mT_s/\tau + T_s)}{R - T_s/\tau} = \frac{T_T - (mT_s/\tau + T_s)}{R_M - T_s/\tau} \qquad R \geq T_s/\tau$$

Substituting for T from equation (1), it is easily shown that this formulation reduces to equation (9). Thus, we have some assurance that the derivation of equation (9) does not imply any capacities that a fish could not be reasonably expected to possess. Accordingly, it appears that equation (9) provides an adequate, and biologically plausible, description of cod feeding and growth in laboratory environments.

NATURAL ENVIRONMENTS

I now consider the different situation in natural environments, where ration levels are determined by the interaction of the fish with its available prey, rather than by an experimental protocol. In this case, two important papers on optimal foraging theory for active predators (Ware 1975, 1978) provide useful guidance. Ware provided persuasive evidence that predatory fish in nature allocate their foraging activities in such a way as to maximize Δw, under any particular conditions of prey availability. Specifically, he showed that the swimming speeds of actively foraging fish vary so as to produce the maximum Δw achievable under the circumstances. Ware did not indicate if foraging time could potentially vary, and thus he did not directly tell us whether the foraging expenditure T_F is similarly optimized to produce a maximum growth rate. I make that assumption here, however, on the grounds that it follows implicitly from Ware's arguments. That is, I conclude that actively predatory fish in nature regulate T_F so as to maximize Δw for a given prey availability.

If this is so, it is useful to consider the relation of equation (9) to Ware's conclusions. Equation (1) can be expressed as

$$\Delta w_M = pR_M - T_T$$

where Δw_M is defined as the maximum possible rate of surplus energy accumulation. Substituting this in equation (9), and rearranging, gives

$$\frac{\tau R - T_s}{\tau R_M - T_s} = \frac{\Delta w}{\Delta w_M} \qquad R \geq T_s/\tau$$

From equation (5), the further substitutions

$$\tau R - T_s = T_F + \Delta w$$

and

$$\tau R_M - T_s = T_{FM}' + \Delta w_M$$

can be made, and then, simplifying, we have

$$\frac{T_F}{T_{FM}'} = \frac{\Delta w}{\Delta w_M}$$

That is, average relative activity expenditure varies, food availability permitting, in direct proportion to average relative surplus energy accumulation.

The structure of equation (10), and thus equation (9), appears relevant to natural environments. As noted above, Ware's examination of optimal foraging theory shows that fish forage at the speeds appropriate to deriving maximum production, over a natural range of prey availabilities. Accepting the further implication that foraging activity itself, i.e. the time spent foraging as well as the speed with which it is conducted, is either constant or similarly optimized to produce maximum production, then average T_F must be directly coupled with average Δw. In particular, where prey are freely available it follows that $T_F \rightarrow T_{FM}'$ as $\Delta w \rightarrow \Delta w_M$, and conversely, where prey become scarce, that $T_F \rightarrow 0$ as $\Delta w \rightarrow 0$. The most direct expression of Ware's findings is the linear relation set out in equation (10). This is not to suggest that it is the only potential expression consistent with Ware's analysis, merely that it is the simplest. Moreover, Ware's optimality approach inevitably raises the larger question of what is actually being optimized in nature; the independent convergence of Ware's conclusions with my analysis is reassuring. Accordingly, there is reason to believe that equation (9), although derived from laboratory evidence, may be equally applicable to active predators in natural environments, despite the very different metabolic costs represented by T_F between the two environments.

It is not immediately clear why similar T_F/R relationships should exist in both laboratory and field situations or, indeed, why regular patterns should emerge at all in the laboratory. Quite apart from Ware's rigorous analysis, there are intuitive, a priori grounds to expect a relationship in the field, where foraging costs for active predators ought to be a major activity component, directly associated with ration intake. Foraging

costs are seldom a major component in experimental designs, however, except in those few cases where capably fugitive, living prey are offered (e.g. Baldwin 1956). The laboratory evidence appears to be saying that fish are maximally active at maximum rations, and reduce their activity proportionately to zero as rations are reduced to the maintenance level. I speculate that the activity levels mounted by aquarium fish in proportion to their ration levels may represent some form of spontaneous "displacement" activity, corresponding to the foraging and other activity that would otherwise have been exerted in natural environments. Regardless of their cause, however, the existence of T_F/R linearities in laboratory experiments gives further reason for confidence in their existence in natural environments, supplementing the independent evidence for their existence reviewed above. Majkowski and Waiwood (1981) have recently published broadly similar conclusions concerning the association of metabolic expenditure with ration level.

Cod Ration in Nature

The strongest assurance of the validity of equation (9) would come from unequivocal tests with independent field estimates of R. Unfortunately, published field estimates of R are neither adequately precise nor satisfactorily accurate for a definitive test with any fish species; indeed it is because of current methodological limitations that the present model seemed worth developing. With this qualification, however, there is an abundance of fish ration estimates in the literature.

Jones (1978) provided ration estimates, based on stomach analysis, for North Sea and Faroe Island cod, and Daan (1973) gave similar estimates for North Sea cod. Jones also presented results of a metabolic model which is basically similar to the present one, except that it uses an empirical function to provide for activity costs rather than the simpler, analytical form used here. Estimates from Jones' model, in addition to his stomach analysis data, are compared in what follows with estimates generated by my model. Furthermore, by making the somewhat questionable assumption that cod and haddock are physiologically similar, I have used metabolic coefficients for cod to compare results from my model with ration estimates for North Sea and Faroe Island haddock, also prepared by Jones (1978).

In applying equation (9) to these field data, I used the same coefficients as were applied to the earlier laboratory data, with two modifications. In the first place, the assimilation coefficient, $p = 0.98$, reported by Edwards et al. (1972) is clearly too high even for the highly digestible diet they offered. Although I used that value for estimates with their data (Fig. 2 and 3), to avoid having to modify their associated data, it seemed better to select a lower value for field application. As a somewhat more realistic choice for wild cod and haddock, I elected to use $p = 0.9$ (Table 1).

The second modification is a consequence of the first one. In view of the evidence that fish increase their ingestion rate to compensate for decreased energy density of their diet (cf. Peter 1979) it seemed reasonable that R_M would itself be affected by the assimilation coefficient. To modify R_M, I assumed that the product pR_M is constant, in which case the new $R_M = 6.5$.

I have no firm evidence that either of these modifications

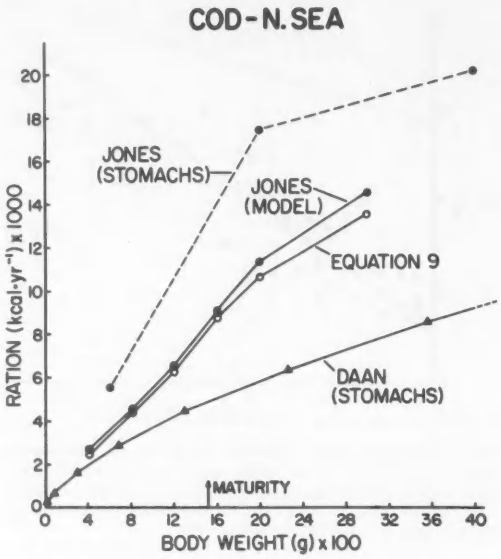

FIG. 4. Ration estimates for North Sea cod derived from stomach analyses by Jones (1978) and Daan (1973) compared with estimates from Jones' model and my equation (9). Estimates with my model used the coefficients set out in Table 1, together with temperature, age at maturity, and fecundity conversions (for estimation of surplus energy, Δw) as given by Jones. Energy units in kcal·d^{-1} are equivalent to 4.184×10^3 J·d^{-1}.

is in fact an improvement. Indeed, the relatively large uncertainty about the validity of the independent test data makes it difficult to determine whether any refinement of the crude coefficients I used would in fact be an improvement. The field comparisons could just as easily have been made without change from the laboratory estimates. but it did seem reasonable and justifiable to avoid an assimilation coefficient that is clearly unrealistic for field conditions.

Refined tests of the model must await the availability of precise, accurate ration estimates. In the interim, the comparisons depicted in Fig. 4–7 indicate that equation (9), armed with approximate coefficient values, generates ration estimates that are of the same magnitude as independent estimates derived from stomach analyses. Moveover, the estimates from equation (9) compare closely with those from Jones' empirically based model.

Further comparisons of interest can be made. The relative levels of ration and activity metabolism routinely attained by natural populations are not well-known. For Jones' production data for North Sea cod, my model estimated that R ranged from 54 to 71% of maximum rations, calculated as annual averages for fish of various body sizes. Comparable estimates for the Faroe cod vary similarly with body size, over the range 52–62% of maximum rations. These values may seem relatively high, but the North Sea cod, in particular, are among the faster-growing cod stocks that have been studied and a relatively high ration intake therefore seems reasonable. Food availability must vary substantially within the course of

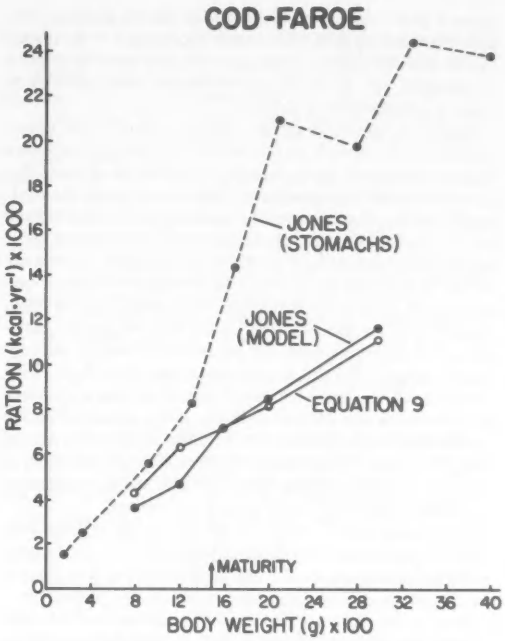

FIG. 5. Ration estimates for Faroe cod, comparing Jones' (1978) stomach analysis and model estimates with equation (9). See caption to Fig. 4.

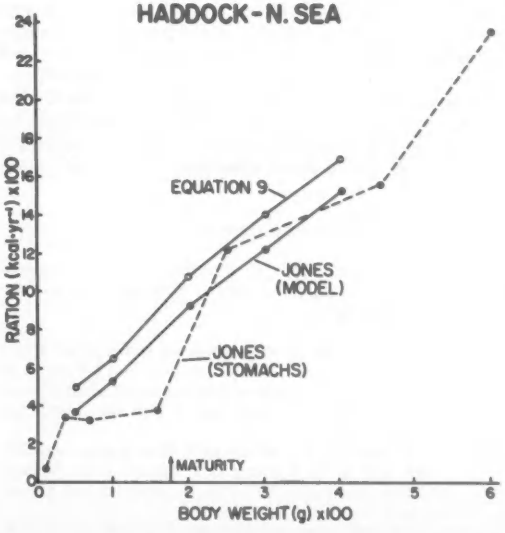

FIG. 6. Ration estimates for North Sea haddock. See caption to Fig. 5. The estimates made with equation (9) assume that haddock are physiologically identical with cod, which is at best an approximation.

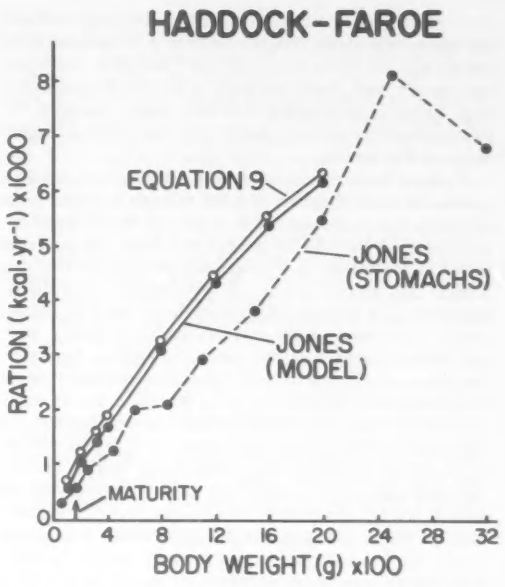

FIG. 7. Ration estimates for Faroe haddock. See caption to Fig. 6.

a year, from which it follows that some size-classes of these cod must at times approach maximum feeding rates, if the above annual averages are maintained.

The model enables similar comparisons of total metabolic expenditures, relative to standard metabolism. Estimates of metabolism for the North Sea cod range from 2.6 to 3.4 T_s, and from 2.5 to 2.9 T_s for the Faroe cod. Kerr (1971c) and Ware (1975) have concluded, on the premise of optimal foraging considerations, that the metabolic expenditures of wild fishes will ordinarily be in the range of $2-3\ T_s$. The foregoing estimates are in the upper portion of that range, which is again consistent with the relatively high rates of growth of these stocks.

Discussion

The utility of equation (9) depends entirely upon its ability to generate accurate estimates of field metabolism or rations for a variety of fish species that forage actively for their prey. The results offered here suggest that it does so, but the validity of the model is by no means confirmed by these comparisons. In fact, the model has been described here in the hope that investigators in possession of accurate food consumption or field metabolism estimates will be interested in applying their data to definitive tests of the model.

In brief, suitable test data comprise, first, a set of surplus energy estimates (Δw, i.e. somatic plus reproductive accumulation) for use in the model, and, second, independent estimates of ration input or field metabolism, for comparison with model estimates, both measured in common energy units over common intervals of time for the same stock of active predators. Further, the fish species chosen must be one of the numerous species for which conventional, laboratory esti-

mates of metabolic parameters are available: α_s, α_T, and γ of the metabolism−body weight relationship; a means of estimating R_M; the assimilation (p) and calorigenic (m) components of τ; and, finally, a means of temperature correction (e.g. Krogh or exponential function) where necessary. Of these, suitable R_M estimates may be the least widely available for some fish species.

The need for independent test data of high quality has been stressed because there are a priori reasons to suspect that relatively high resolution will be necessary to distinguish between real and spurious fits to the model. In the first place, the model is constrained to generate estimates that at least fall within the known realm of physiological possibility; Nakashima and Leggett (1978) have shown that a significant portion of published ration estimates, based on stomach analysis, do not satisfy even this primitive criterion. Moreover, the general tendency of the model regardless of whether or not its formulation is correct, is to reflect processes that we know must occur. That is, the model predicts a general tendency for metabolic level to increase with ration level, in part because of increased calorigenic (SDA) effect and in part because increased prey ingestion rate must to some degree entail increased activity metabolism for an active predator. Accordingly, relatively good precision will be necessary to determine whether the formulation given as equation (9) in fact correctly describes these processes in nature.

The model offered here is not radically new; rather it represents a further evolution toward generalization of a variety of its predecessors. Its primary advantage consists in the way that activity metabolism is handled. This can most readily be seen by comparison with Jones' model, discussed above. Other differences aside, the major change offered here is that activity metabolism is given in a general, analytical formulation rather than the specific empirical form used by Jones. It is for this reason that the two models produce similar results. In effect what has been gained in the present model is to substitute the need for estimation of activity metabolism, which is known to be relatively labile, for the relatively more stable R_M which seems more readily predictable for given conditions.

If further testing should confirm its validity, the principle advantages offered by the present model are that it is both simpler and more general than its predecessors, owing to its simplification of the ration−activity relationship. The effective scope for its potential applicability is thereby considerably broadened, to encompass a variety of data sets which prior models could not adequately treat, for want of detailed information.

The model has been developed here in a form consistent with Δw as the available input data and R as the desired output. I have done so in the belief that these are respectively the most commonly available input and the most commonly sought output. Used in conjunction with indices of species abundance, the present form lends itself, for example, to analysis of the impact of multispecies fisheries upon common prey resources.

Other formulations of the model are easy to derive, with solutions in the form of T or Δw. Both forms may be of interest in particular situations. The fact that solution for Δw entails knowledge of R or T is of interest in terms of what Ricker (1979) concludes is the intractable problem of developing a generalized growth model for fishery analysis. The present model suggests that suitably generalized forms indeed can be derived, but that it appears necessary to do so in terms of variables (R, T) which are inherently more difficult to observe directly than is Δw itself.

Whatever specific form the model is cast in, the development offered here is certain to distress some physiologists because of several approximations that have been used. The use of a constant power index γ, regardless of metabolic level, and the assumption of a constant assimilation coefficient p are two examples of such approximations. I have made these assumptions because they greatly simplify expression and use of the model, not because they are necessary. Indeed, any measure of complexity that seems warranted could be introduced to any coefficient of the model. I do not believe, however, that such complications are often justified in the ecological context. The ensuing improvement of the model estimates would be illusory, in my view, unless the independent test data are of sufficient accuracy as to permit objective confirmation of the justification for added complexity. As was stressed earlier, I do not believe such conditions often exist as yet, and I therefore suggest that simplicity and approximation are usually preferable in the ecological context.

For similar reasons, no effort has been made to tinker with the coefficients used to improve the model correspondance with field data (Fig. 4−7). The essential point is to demonstrate that an a priori selection of reasonable values gives results of the right magnitude. In the absence of objective reasons to modify coefficients, there is little to be gained by doing so.

Finally, the present considerations suggest a general conclusion of interest to those engaged in fishery data collection. For reasons of convenience, many growth data are collected in terms of body length increments, sometimes (not always) with provision for conversions to body weights and (less often) gonad weights. Clearly, current practice is inadequate if serious progress is to be made in bioenergetic analysis of multispecies fisheries. Body weights must be collected routinely, together with seasonal energy equivalents (MacKinnon 1972) and, because reproductive effort is by no means the simple invariate proportion of body size we often suppose it to be (Ware 1980), gonad observations must also become routine.

Acknowledgments

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Bioconcentration of a Hexachlorobiphenyl in Great Lakes Planktonic Algae

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LEDERMAN, T. C., AND G-Y. RHEE. 1982. Bioconcentration of a hexachlorobiphenyl in Great Lakes planktonic algae. Can. J. Fish. Aquat. Sci. 39: 380–387.

The bioconcentration of 2,4,5,2′,4′,5′-hexachlorobiphenyl (HCB) was examined in the Great Lakes algae *Fragilaria crotonensis*, *Ankistrodesmus falcatus*, and *Microcystis* sp. The bioconcentration factors varied from species to species, whether they were expressed in terms of cell number, dry weight, cellular carbon, or cellular lipid. The factors were in the range of 10^5-10^6 and increased with decreasing biomass. The existence of a mucilage layer in *F. crotonensis* was associated with a twofold increase in the bioconcentration factor. Surface adsorption appeared to contribute only slightly to the bioaccumulation of HCB. HCB desorbed from all species but at a much slower rate than its adsorption.

Key words: bioconcentration, bioaccumulation, polychlorinated biphenyls, hexachlorobiphenyl, adsorption, desorption, algae

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Nous avons examiné la bioconcentration de 2,4,5,2′,4′,5′-hexachlorobiphényl (HCB) dans les algues *Fragilaria crotonensis*, *Ankistrodesmus falcatus* et *Microcystis* sp. des Grands Lacs. Les facteurs de bioconcentration varient d'une espèce à l'autre, qu'ils soient exprimés en termes de nombre de cellules, de poids sec, de carbone cellulaire ou de lipides cellulaires. Ces facteurs se situent dans une gamme de 10^5 à 10^6 et augmentent à mesure que diminue la biomasse. La présence d'une couche mucilagineuse chez *F. crotonensis* est associée au doublement du facteur de bioconcentration. L'adsorption superficielle ne semble contribuer que légèrement à la bioaccumulation de HCB. Cette substance se désorbe chez toutes les espèces, mais à un taux beaucoup plus lent que son adsorption.

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MOST chlorinated synthetic chemicals are potent toxicants to planktonic algae. Because they have extremely low solubility in water and are mostly lipophilic, these compounds concentrate to high levels in biological systems from dilute solutions. Many investigators (e.g. Södergren 1968; Rice and Sikka 1973; Reinert 1972) have shown that chlorinated organic chemicals accumulate in algae by simple chemical absorption, or partitioning. Bioaccumulation of chlorinated compounds varies widely among species and chemicals (Keil et al. 1972; Khan and Khan 1974; Hollister et al. 1975; Neudorf and Khan 1975; Schauberger and Wildman 1977; Paris and Lewis 1976; Wright 1978; Harding and Phillips 1978; Hansen 1979). There have been a few studies on bioconcentration factors for polychlorinated biphenyls (PCBs) in marine planktonic algae (Harding and Phillips 1978; Biggs et al. 1980) but little information is available for freshwater species.

In most investigations the concentrations of chemicals were much higher than their solubilities in water. These concentrations were achieved using carrier solvents such as alcohol and acetone. The high concentration of toxicants raises questions as to the ecological relevance of the investigations, because in natural waters the concentrations of the chemicals are far below solubility limits (Hartung 1975; W. L. Richardson, U.S. EPA Grosse Ile, MI, personal communication).

In the present study we examined the absorption and desorption characteristics of PCBs using the hexachloroisomer 2,4,5,2′,4′,5′-hexachlorobiphenyl (HCB) at concentrations below its aqueous saturation in three species of Great Lakes algae. This isomer was chosen for its environmental ubiquity and the ease of measurement of an available ^{14}C-labeled compound.

Materials and Methods

Axenic stock cultures of the Great Lakes algae *Fragilaria crotonensis* (obtained from D. Tilman, University of Minnesota, Minneapolis, MN) and *Ankistrodesmus falcatus* and *Microcystis* sp. (isolated in our laboratory from Saginaw Bay, Lake Huron) were grown in batches in 8 L of the defined

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inorganic medium of Guillard and Lorenzen (1972) modified by Rhee and Gotham (1981).

All glassware used for the experiments was washed in 9 mol/L sulfuric acid, rinsed in deionized water, washed with acetone, rinsed thoroughly with glass-distilled water, and autoclaved.

A concentrated stock solution of [^{14}C]HCB (New England Nuclear) was prepared as follows: a predetermined amount of the isomer dissolved in acetone was deposited onto the bottom of a 12-L carboy. After the acetone evaporated, 8 L of glass-distilled water was added, and the carboy was sealed with a rubber stopper which had a silicone rubber siphon and an air outlet with a filter. The air outlet filter, a HCB trap, was 10 cm of glass tubing (6 mm o.d.) filled with activated Florisil and cotton. HCB in the carboy was solubilized by autoclaving the bottle at 121°C for about 30 min. The resulting concentrations of HCB had a mean of 3 μg/L. The concentration in this stock remained constant for more than 2 mo.

The stock solution was added aseptically to a sterile, concentrated culture medium to produce a medium containing desired concentrations of nutrient salts and HCB.

For absorption and desorption experiments, exponentially growing *F. crotonensis* was harvested by centrifugation and divided into five equal portions. These portions received various treatments, as follows: (1) used as intact live cells in full-chain length (50−70 cells/chain); (2) sonicated to break up the chains (7−12 cells/chain); (3) heat-killed at 70°C for 10 min; (4) treated with 0.05 mol/L HCl (0.2 mL of HCl/2 mL of cells) and left in hot water (70°C) for 5 min (this treatment killed the cells and at the same time stripped the mucilage layer from the chain; there was no change in average chain length with either heat killing or the acid stripping); (5) used to prepare frustules according to Reimann et al. (1965).

Exponentially growing cultures of *A. falcatus* and *Microcystis* sp. were divided into two aliquots for live and heat-killed cell preparations.

The various cell preparations were centrifuged and resuspended in medium containing HCB at 1 μg/L. The cultures were sampled at predetermined intervals and assayed for total HCB (dissolved plus particulate), cellular HCB, and dissolved HCB. To measure HCB in the particulate (cellular) and liquid fractions, a 5-mL sample was centrifuged in a 15-mL Corex centrifuge tube. A 3-mL sample of the supernatant was delivered into a liquid scintillation vial for measurement of residual HCB in the medium. The remaining supernatant and cell pellet were transferred to a liquid scintillation vial. The centrifuge tube was then rinsed with 1 mL of glass-distilled water, and the rinse was combined with the cell pellet in the scintillation vial. The scintillant, Aquasol (New England Nuclear), was added to each sample to form a gel, and radioactivity was counted by a Beckman liquid scintillation counter. The counts were corrected for background; quench corrections were made by the channels-ratio, external-standard method. Cellular HCB was determined by subtracting the activity in 2 mL of residual HCB from the activity of the sample containing the cell pellet.

Adsorption of the HCB to the glass surfaces was less than 5% for the culture and less than 1% for centrifuge tubes. Without algae, however, the adsorption to the flasks was considerably higher. The total recovery of HCB from the various compartments of the experimental system was better than 92%.

During each experiment *A. falcatus* and *Microcystis* sp. were counted once or twice a day with a Coulter counter (model IIa with population accessory). *Fragilaria crotonensis* was counted, after sonication to break up long chains, in a Fuchs-Rosenthal, Ultra Plane counting chamber. *Microcystis* sp. grew as single cells without developing into coenobia. In all species heat killing caused no change in the size distribution.

Dry weight was measured by weighing a washed cell pellet which had been dried to constant weight at 90°C. Cellular carbon was measured with a total organic carbon analyzer (Beckman model 915B). Lipids were extracted in a modification of the one-step extraction and purification method of Bligh and Dyer (1959); they were extracted into a water:chloroform:methanol (0.8:1.0:2.0, v/v) mixture and left overnight in a freezer. The sample was filtered, and the filter was rinsed with the same volume of chloroform as used in the mixed solvent. A volume of glass-distilled water equal to the chloroform was then added to the filtrate, and the lipids were separated into the chloroform layer. This chloroform was removed, dried by bubbling N_2 into it, and weighed for lipids.

The bioconcentration factor was calculated at equilibrium as (mg HCB/g dry weight) ÷ (mg HCB/mL medium). The equilibrium point for both absorption and desorption was determined by plotting the total particulate HCB against time. When the particulate HCB did not change with time an equilibrium was assumed. The bioconcentration factor was also expressed as the mass of the absorbent per gram of carbon or lipid, instead of dry weight.

Results

ABSORPTION

Short-term uptake of HCB by *F. crotonensis* was investigated with long- and short-chained live cells, heat-killed cells, and frustules. The frustules were used for an indirect evaluation of the physical adsorption to the cell surface. Because *F. crotonensis* is a chain-forming species, the possible effects of chain length on bioaccumulation (smaller length chains have a larger ratio of surface to volume) were evaluated by comparing the uptake by short-chained (sonicated) cells with that of long-chained (unsonicated) cells.

There appears to be no significant difference at 95% among the rates between 15 and 60 min of uptake by short-chained, long-chained, and heat-killed cells (Fig. 1a). The chain length of the dead cells was unaltered by the process of heat killing and thus was comparable with that of the live, long-chained cells. The uptake rate for the frustules (Fig. 1b) was about 30% of the other cell preparations.

The bioaccumulation of HCB at the end of the experiments, i.e. at 5 h, was appreciably higher in short-chained than long-chained cells (the standard error of each concentration was always less than 15% of the mean), but the frustules accumulated an order of magnitude less HCB than did the other preparations. Uptake was continuing at 5 h, as the HCB per cell was increasing in all preparations except the frustules.

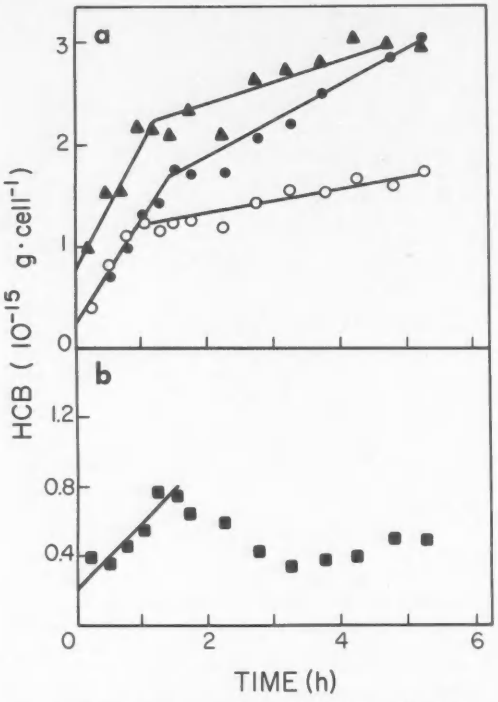

FIG. 1. Time course of uptake of 2,4,5,2′,4′,5′-hexachlorobiphenyl (HCB) by (a) long-chained (○), short-chained (●), and dead cells (▲) and (b) frustules (■) of *Fragilaria crotonensis*.

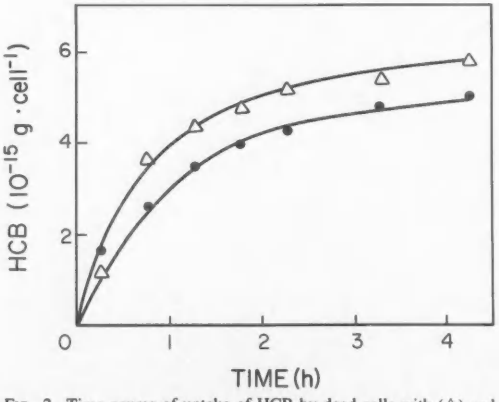

FIG. 2. Time course of uptake of HCB by dead cells with (△) and without (●) a mucilage layer in *Fragilaria crotonensis*.

It appears that the difference in bioaccumulation between dead and live, long-chained cells was primarily due to the amount of uptake which occurred between 0 and 15 min. Uptake during this period was always higher in dead cells (a phenomenon common to dead cells of all species studied,

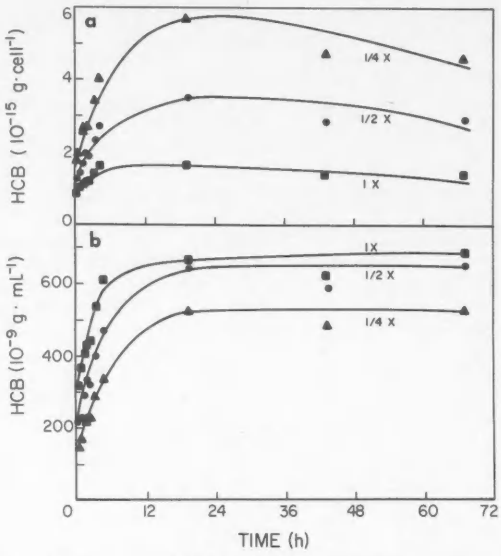

FIG. 3. Time course of HCB uptake by live *Fragilaria crotonensis* at three cell densities: 80 000 (■), 160 000 (●), and 320 000 (▲) cells/mL. (a) HCB/cell; (b) total particulate HCB/mL medium.

see below), possibly resulting from the heat denaturation of cellular constituents such as lipids and proteins. Nonetheless, the similarities in the initial uptake rate and in bioaccumulation by live and dead cells demonstrates that HCB uptake probably does not involve a biological transport system.

The difference in bioaccumulation between the long-chained and short-chained cells is not a result of a dissimilarity in uptake during the 0- to 15-min period. Rather, it was caused by the longer linear phase of uptake (15−60 min) by short-chained cells and by their higher rate of uptake after the initial linear phase. The difference in bioaccumulation might not be due simply to the difference in the chain length, as it is not clear what effects sonication had on cellular structures. The longer initial linear phase in sonicated cells could be an indication of alteration or disruption of cellular organization. However, the sonicated populations were viable, although it was not determined whether the fraction of nonviable cells was different from that in nonsonicated cultures.

The effects of the gelatinous layer of the diatom on absorption were determined with dead cells (removal of the layer did not affect the chain length). The rate as well as the total amount of accumulation was higher in cells having the mucilagenous layer (Fig. 2). When bioconcentration factors were calculated at equilibrium (between 16 and 23 h after the start of an experiment), the factor was almost twice as high with mucilage (average 7.19×10^5) as without (3.98×10^5).

In other experiments, which lasted 68 h, possible effects of population size and concentration of adsorbant on the bioconcentration factor were determined. An equilibrium of HCB between the liquid and particulate phases was attained between 6 and 20 h, and the larger the population size, the smaller was the cellular HCB (Fig. 3). The decrease of the

TABLE 1. Bioconcentration factors ($\times 10^5$) at various population densities from absorption experiments.

Species	Live cells			Dead cells			Frustules		
	N[a]	*N*/2	*N*/4	*N*	*N*/2	*N*/4	*N*	*N*/2	*N*/4
Fragilaria crotonensis[b]	1.17	3.13	—	3.25	6.98	7.07	0.38	0.18	0.32
Ankistrodesmus falcatus[c]	6.19	9.59	12.07	15.56	23.14	36.76			
Microcystis sp.[c]	1.29	1.70	2.64	7.14	9.51	10.99			

[a] *N* = culture density: *F. crotonensis*, 320 000/mL; *A. falcatus*, 340 000/mL; *Microcystis* sp., 1100 000/mL.
[b] The equilibration time when the factor was calculated was 19 h for live cells. For dead cells and frustules, it was 19 and 43 h and the values are an average of the two measurements.
[c] The equilibration time for both live and dead cells was 6 h.

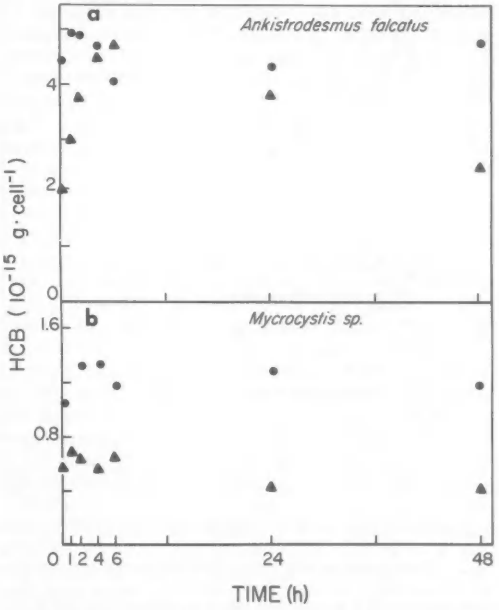

FIG. 4. Time course of HCB uptake by live (▲) and dead (●) *Ankistrodesmus falcatus* and *Microcystis* sp.

cellular HCB after 20 h was due to population growth, as the total particulate HCB remained constant (Fig. 3b). The bioconcentration factors at equilibrium (Table 1) also decreased with increasing population size, and the factors for dead cells were about double those for live cells. The difference between live and dead cells is not due to the increase in population in live cultures during the experiments because the difference was also noted at 6–20 h, when there was little increase in population in the live culture. Moreover, with other species similar differences were found within 2 h (see below).

The bioconcentration factors for frustules were lower by an order of magnitude than the factors for live and dead cells. It appears therefore that adsorption to the cell surface contributes only a little to the bioaccumulation of HCB.

At the equilibrium point the aqueous concentrations of HCB were very low, about 20–40 ng/L.To investigate the magnitude of the bioconcentration factor when the aqueous concentration is high, *Fragilaria* cultures were transferred into fresh HCB medium daily for 7 d. After that time the external HCB concentration reached 630 ng/L, and cell HCB was 13.1×10^{-6} ng/cell, but the bioconcentration factor remained at the same order of magnitude (2.5×10^5).

In *A. falcatus* most uptake took place within 6 h for live cells and 1 h for dead cells (Fig. 4). There was no difference in the amount of uptake between live and dead cells at 6 h. In contrast, uptake was complete within 2 h for both live and dead *Microcystis* cells, but the amount of uptake by dead cells was about twice the amount for live cells. The difference in cellular HCB between live and dead *A. falcatus* after 6 h was due to the increasing culture density in the live culture. However, the difference between live and dead *Microcystis* sp. was not attributable to multiplication of the algae, as the difference in cellular HCB appeared in the very early phase of the experiments. There was a significant difference (all paired differences were significant at greater than 95%) in bioconcentration factors and thus in absorptive capacity between live and dead cells (Table 1). The factor was significantly greater in dead cells and also increased with increasing culture density, as in *F. crotonensis*.

Within the concentration range of HCB in the present experiments, i.e. 1 μg/L, it was not possible to discern differences in the external HCB concentration at equilibrium in experiments with different initial concentrations. Therefore absorption isotherms could not be calculated.

For each species the bioconcentration factors were much larger for dead than for live cells, and it decreased with increasing biomass per unit volume of culture (Fig. 5). On a dry weight basis, comparing live with live or dead with dead cells, the factor for *A. falcatus* was much larger than those for *F. crotonensis* and *Microcystis* sp., but there was little or no difference between the latter species. On the basis of carbon or lipid the factor for dead *Microcystis* was very close to that of dead *A. falcatus*, while *F. crotonensis* had the lowest factor. For live cultures *A. falcatus* had a significantly larger factor than those for *F. crotonensis* and *Microcystis* sp. There was little difference between the latter two species.

DESORPTION

Desorption of HCB was examined in two sets of experiments. In one set, HCB-labeled cells were harvested immediately after the termination of the absorption experiments; the cells were resuspended in HCB-free medium, and the time course of desorption was followed (Fig. 6). Desorption rates were much lower than absorption rates. The bioconcentration

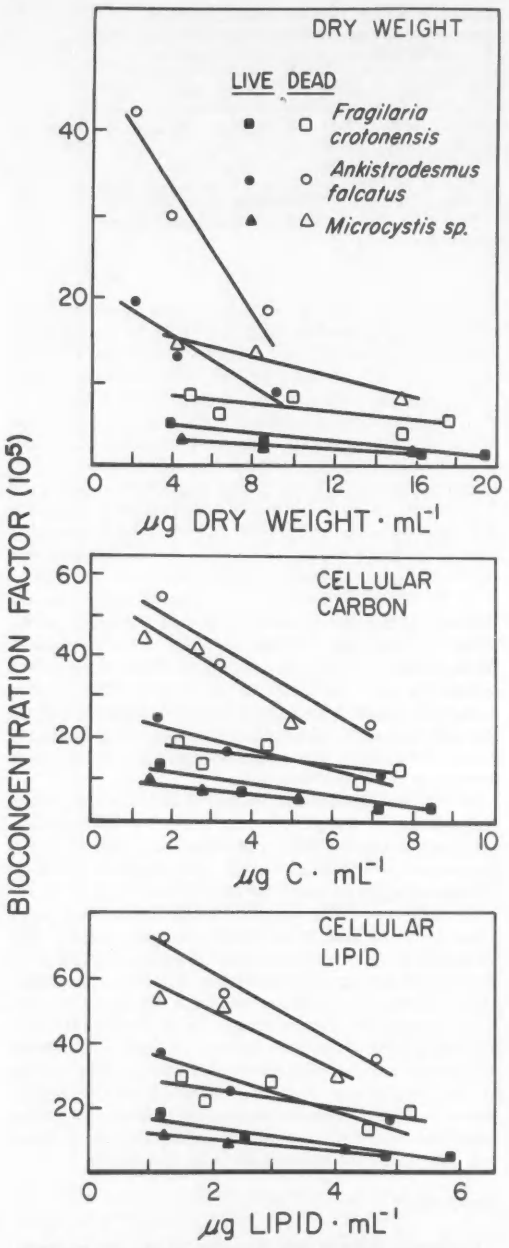

FIG. 5. Bioconcentration factors from the absorption experiments for live and dead *Fragilaria crotonensis*, *Ankistrodesmus falcatus*, and *Microcystis* sp. in terms of dry weight, cellular carbon, and cellular lipid. These factors were calculated at equilibrium and are the mass of HCB per unit weight of biomass relative to the mass of HCB per unit weight of medium.

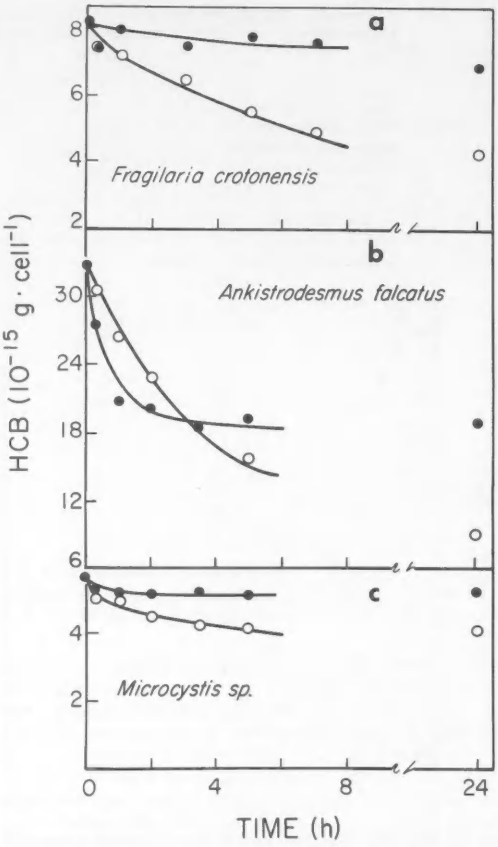

FIG. 6. Time course of desorption of HCB from dead *Fragilaria crotonensis*, *Ankistrodesmus falcatus*, and *Microcystis* sp. Cells were resuspended in HCB-free medium (●) or were centrifuged and resuspended in fresh, HCB-free medium after each sampling (○).

factors determined at equilibrium in these experiments were also greater than the factors determined at equilibrium in the absorption experiments (Table 2). There were also species differences in desorption, with *A. falcatus* exhibiting the greatest amount of desorption and *Microcystis* the least.

In other sets of experiments HCB-labeled cells were suspended in HCB-free medium, and after sampling the medium was exchanged with fresh medium (Fig. 6). In resuspended cultures there was considerable additional desorption by *A. falcatus* and *F. crotonensis* but relatively little by *Microcystis* sp.

Discussion

The present investigation is different from most other studies in that the concentrations of the isomer were below its saturation limit in water (1−9 μg/L; see Wallnofer et al. 1973; Haque and Schmedding 1975) and were close to the

concentrations in natural waters. Also the solutions were prepared without carrier solvents such as acetone or alcohol. Most earlier investigations, in contrast, employed artificially high concentrations of toxicants which were attained using carrier solvents, whose effects on the partitioning behavior of absorbents had not been determined.

Nevertheless the bioconcentration factors obtained for our test species are generally of the same order of magnitude as factors obtained for marine species by other investigators. Harding and Phillips (1978) studied 11 species of marine algae in a medium prepared using acetone to dissolve PCBs. Factors for most algae were 10^5 on a volume/volume basis. Our bioconcentration factors for *A. falcatus* and *Microcystis* sp. fall within the same magnitude when calculated on the same basis. The factor for *F. crotonensis* varies depending on whether or not the mucilaginous layer is included in the total volume. With the layer (1070 μm^3/cell) the factor is on the order of 10^4; without the layer (260 μm^3/cell) it is on the order of 10^5. Biggs et al. (1980) reported the bioconcentration factor of PCBs in *Skeletonema costatum* at 2×10^4. However, comparisons between studies are difficult because of different experimental conditions, especially the culture densities.

The bioconcentration factor increases with decreasing culture density (Fig. 5). This phenomenon has also been observed by other investigators in different species of algae (Rice and Sikka 1973; Neudorf and Khan 1975) and for various adsorbing solids (O'Connor and Connolly 1980). This variation was noted in our studies whether the concentration factor was expressed per dry weight, cellular carbon, or cellular lipid (Fig. 5). The relationship of the factor to cell numbers is also the same as with other parameters, as the relationship between cell number and the other parameters is constant for a given species. The fact that inhibitory effects of PCBs on net photosynthesis are more pronounced in dilute cell suspensions (Cole and Plapp 1974) most likely results from the variation in bioconcentration factors with culture density. Therefore, in interpreting toxicity data or comparing inhibitory effects of toxicants among species, one must take into account the effect of biomass per volume on the bioconcentration factor.

One must also consider these effects when extrapolating laboratory results to natural environments. For example, even if the concentrations of toxicants in natural waters are less than the toxic level determined in the laboratory, this may not mean that the environmental concentrations are nontoxic, because the densities of natural populations and other particulate materials are seldom as high as the densities of laboratory cultures. As the bioconcentration factor indicates, the direction of equilibrium for PCBs is extremely favorable to bioconcentration in algal cells, resulting in very low aqueous concentrations. In light of this fact and of the effect of population density on bioconcentration, it is important that the toxicant concentrations be reported and compared on an appropriate biomass basis, such as cell mass, cellular C, or cellular lipid.

Correlations have been shown between solubility, octanol/water partition coefficient, and bioconcentration in fish (Neely et al. 1974; Chiou et al. 1977; Metcalf et al. 1975) and in algae (Hutchinson et al. 1980). In establishing such empirical relationships for phytoplankton, one must also consider the dependence of the bioconcentration factor on

TABLE 2. Bioconcentration factors ($\times 10^5$) at various population densities from desorption experiments.

Species[a]	Parameters	Live cells			Dead cells			Frustules		
Fragilaria crotonensis	Cell numbers ($\times 10^3$/mL)	400	200	100	250	125	62	200	100	50
	Bioconcentration factor	4.89	8.25	7.69	—	8.13	15.4	0.25	0.37	—
Ankistrodesmus falcatus	Cell numbers ($\times 10^3$/mL)	590	290	267						
	Bioconcentration factor	36.88	33.19	39.88						
Microcystis sp.	Cell numbers ($\times 10^3$/mL)	2140	2567	2281						
	Bioconcentration factor	7.81	4.24	6.20						

[a]For equilibration times see Table 1.

population density.

The dissimilarities in the bioconcentration factor between species may be due to differences in the cell size, morphology, and chemical composition of the organism. Hiraizumi et al. (1979) reported that PCB partition coefficients are inversely related to the average particle size and linearly related to the surface area for the same adsorbent. The partition coefficient is also affected by the organic content of the adsorbent (Hiraizumi et al. 1979; Weber et al. 1980) but does not appear to be influenced by the initial concentration of absorbate (Reinert 1972; O'Connor and Connolly 1980). We have observed the same effects in our studies with *A. falcatus*.

The increase of absorption by layers of mucilage was also reported for uptake of lindane by *Chlorella* (Hansen 1979). This has important ecological implications, as large quantities of amorphous, filter-clogging, gelatinous materials are present in many aquatic environments (Palmer 1964; W. R. Swain, U.S. EPA, Grosse Ile, MI, personal communication), and they will compete with organisms for toxicants.

The time course shown in Fig. 6 indicates that absorption may not be a completely reversible phenomenon. The bioconcentration factor for absorption does not apply to desorption, and once the HCB is partitioned into organic material, a certain fraction of the compound becomes firmly bound to cell constituents. This phenomenon is also indicated by higher bioconcentration factors when estimated from desorption compared with absorption. Picer et al. (1977) and Hiraizumi et al. (1979) also found that the rate of desorption is much slower than that of absorption. Furthermore, Biggs et al. (1980) have shown that a 5-d dialysis did not completely remove PCBs from a mixed assemblage of phytoplankton. To explain the differences between adsorption and desorption isotherms D. DiToro (Manhattan College, New York, NY, personal communication) recently advanced a kinetic model postulating the existence of two components in adsorption and desorption, i.e. exchangeable and nonexchangeable components of the adsorbate with different partition coefficients.

In all species investigated the dead cells accumulated more HCB than did the live cells. A similar observation was reported by Urey et al. (1976). Although we cannot offer a definite physical or biochemical explanation, this difference may be due to heat-denaturation of cellular constituents such as lipids and proteins and the disintegration of subcellular organization in dead cells.

The high bioconcentration factors for the three species of algae indicate that HCB will become associated with living as well as nonliving particulate organic matter in natural environments. Such accumulation in organisms can destabilize the aquatic food chain. At the same time, accumulation in living and nonliving particulate matter can contribute to the removal of toxicant from the water column by sedimentation.

Acknowledgments

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Influence of a Hexachlorobiphenyl in Great Lakes Phytoplankton in Continuous Culture

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LEDERMAN, T. C., AND G-Y. RHEE. 1982. Influence of a hexachlorobiphenyl in Great Lakes phytoplankton in continuous culture. Can. J. Fish. Aquat. Sci. 39: 388–394.

The influence of 2,4,5,2′,4′,5′-hexachlorobiphenyl (HCB) on the growth of Great Lakes phytoplankters *Fragilaria crotonensis*, *Ankistrodesmus falcatus*, and *Microcystis* sp. was investigated in continuous culture under nutrient-sufficient and phosphate (P) limited conditions. Growth rate (μ) was inhibited only in *F. crotonensis* at cellular HCB concentrations as low as 4×10^{-8} ng/cell (0.8 μg/g dry weight) in nutrient-sufficient cultures; there appeared to be a dose–response relationship between cellular HCB and μ. *Microcystis* sp. and *A. falcatus* showed no inhibitory effect at cellular HCB levels up to 5×10^{-8} ng/cell (3.6 μg/g dry weight) and 30×10^{-8} ng/cell (11.5 μg/g dry weight), respectively. Under P-limited conditions HCB also affected *F. crotonensis* but not *A. falcatus*. The initial response of *F. crotonensis* to HCB addition was a significant increase in μ, followed by a sharp decline. In both nutrient-rich and P-limited *F. crotonensis* the cellular chlorophyll *a* (chl *a*) concentration decreased with the accumulation of HCB, yet the ^{14}C assimilation rate per unit chl *a* increased. Cellular P concentration in the P-limited cells also decreased with the accumulation of HCB. Such responses were not observed in the other species.

Key words: polychlorinated biphenyls, hexachlorobiphenyl, bioconcentration, Great Lakes, algae, continuous culture

LEDERMAN, T. C., AND G-Y. RHEE. 1982. Influence of a hexachlorobiphenyl in Great Lakes phytoplankton in continuous culture. Can. J. Fish. Aquat. Sci. 39: 388–394.

L'influence de 2,4,5,2′,4′,5′-hexachlorobiphényl (HCB) sur la croissance des phytoplanctontes *Fragilaria crotonensis*, *Ankistrodesmus falcatus* et *Microcystis* sp. des Grands Lacs a été l'objet d'une recherche en culture continue dans des conditions de suffisance de nutriments et de limitation de phosphate (P). Le taux de croissance (μ) n'a été retardé que chez *F. crotonensis* à des concentrations de HCB aussi faibles que 4×10^{-8} ng/cellule (0,8 μg/g de poids sec) dans les cultures avec nutriments suffisants; il semble y avoir une relation dose–réponse entre le HCB cellulaire et μ. Il n'y a aucun signe d'inhibition chez *Microcystis* sp. et *A. falcatus* à des niveaux de HCB cellulaire allant jusqu'à 5×10^{-8} ng/cellule (3,6 μg/g de poids sec) et 30×10^{-8} ng/cellule (11,5 μg/g de poids sec) respectivement. Dans des conditions de P limité, HCB influence également *F. crotonensis* mais non *A. falcatus*. La réponse initiale de *F. crotonensis* à l'addition de HCB est une importante augmentation de μ, suivie d'une brusque diminution. Chez *F. crotonensis* en cultures riches en éléments nutritifs et pauvres en P, la concentration de chlorophylle *a* cellulaire (chl *a*) diminue avec l'accumulation de HCB tandis que le taux d'assimilation du ^{14}C par unité de chl *a* augmente. La concentration de P cellulaire dans des cellules en cultures à P limité diminue également avec l'accumulation de HCB. Nous n'avons pas observé de réponse semblable chez les autres espèces.

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THE toxic effects of polychlorinated biphenyls (PCBs) on phytoplankton have been reported by many investigators (Keil et al. 1971; Fisher and Wurster 1973; Mosser et al. 1974; Larsson and Tillberg 1975; Nimmo et al. 1975; Harding 1976; Harding and Phillips 1978a; O'Connors et al. 1978). These synthetic chemicals accumulate to high concentrations in biological systems from a dilute solution and bioaccumulation appears to occur not by active transport, but by physical absorption, which can be described by the Freundlich isotherm (e.g. Harding and Phillips 1978b).

Most studies of toxic effects have used batch cultures in

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which the concentrations of the toxicants far exceed their aqueous solubilities; these high concentrations were achieved using various carrier solvents. In such investigations toxic effects were expressed in terms of the initial concentrations of toxicants in the medium.

Besides the problem of artificially high concentrations and the use of solvents (Lederman and Rhee 1982), measurement of toxicity as a function of medium concentrations may be of little value, because bioaccumulation in cells varies inversely with the amount of biomass, even at the same toxicant concentrations (Keil et al. 1972; Rice and Sikka 1973; Neudorf and Khan 1975; Lederman and Rhee 1982). Moreover the relationship between the partition coefficient and concentrations of various solids appears to be very complex (O'Connor and Connolly 1980) and not yet clearly understood.

In the light of the environmental ubiquity of PCBs, it is essential to understand their toxic effects in terms that can be related to natural conditions. In our present studies, therefore, we investigated the effects of 2,4,5,2′,4′,5′-hexachlorobiphenyl (HCB) without solvents and at low concentrations close to those which occur in natural waters. This investigation was carried out under optimal growth (nutrient-sufficient) conditions to determine the effects of the toxicant without other environmental stresses. Parallel studies were also carried out under phosphate (P) limitation, a condition of nutrient stress that occurs most often in freshwater environments. The effects were expressed as a function of cellular concentrations of the toxicant, although external concentrations were also determined.

Materials and Methods

Axenic cultures of the Great Lakes algae *Fragilaria crotonensis*, *Ankistrodesmus falcatus*, and *Microcystis* sp. described in Lederman and Rhee (1982) were grown in P-limited chemostats and nutrient-sufficient turbidostats. The culture medium and continuous culture systems have been described elsewhere (Rhee and Gotham 1981; Rhee 1980). Phosphate was 50 μmol/L in the nutrient-sufficient medium and 1 μmol/L in the P-limited medium. In the *Mycrocystis* medium, NH_4Cl was substituted for $NaNO_3$, as this alga cannot utilize nitrate. The preparation of medium containing [^{14}C]HCB is reported in Lederman and Rhee (1982).

The cultures were grown at 18 ± 1°C in continuous light from a circular cool-white fluorescent lamp. The average irradiance in the culture was 25 W/m^2.

The cultures were first grown in HCB-free medium. Once they reached steady state, samples were taken daily for 2 or 3 d to obtain base-line information. The reservoir medium was then replaced with one containing 0.2−1.2 μg/L HCB. In chemostats inhibitory effects on growth rate (μ) were observed as a reduction in culture density, as

$$(1) \quad \mu = D + ln\,(X_1/X_2)/t$$

where D is the dilution rate, t is time, and X_1 and X_2 are cell numbers at time 1 and 2, respectively. In turbidostats a constant cell density is maintained by feedback regulation of dilution of the cultures; therefore, a change in μ was observed as a change in the volume of overflow.

A daily sample of 80 mL was taken from 1-L cultures for analyses of dissolved, particulate, and total HCB, chlorophyll *a* and in vivo fluorescence, and cellular C, N, P, and ATP. The HCB and P in the reservoir were also measured.

[^{14}C]HCB concentrations were determined with a liquid scintillation counter (Packard Tri-Carb). However, it was not determined if the organisms produced any metabolites of HCB. Chlorophyll *a* (chl *a*) was measured in acetone extracts of *F. crotonensis* and *Microcystis* and in chloroform:methanol (2:1, v/v) extracts of *A. falcatus* (L.W. Wood, N.Y.S. Dep. of Health, personal communication). Duplicate samples extracted in a dark freezer overnight were read in a fluorometer. Chl *a* concentrations were expressed in arbitrary units. Cellular C was determined with a carbon analyzer (Beckman 915B). Cellular P was measured according to Murphy and Riley (1962) after persulfate digestion (Menzel and Corwin 1965). Cellular N was measured according to Raveh and Avnimelech (1979) and ATP by the procedure of Jones and Simon (1977).

Because large samples were required for lipid analysis, daily overflows from chemostats and turbidostats were collected in large bottles placed in Styrofoam boxes packed with ice. These overflow samples were harvested by centrifugation and analyzed for the total lipids by a modification (Lederman and Rhee 1982) of the one-step extraction−purification method of Bligh and Dyer (1959).

During several experiments a 100-mL aliquot of the culture was taken for measurement of C fixation by the ^{14}C technique. The rate was determined as the slope of the plot of ^{14}C fixed vs. time.

Results

In all nutrient-sufficient turbidostat cultures of *F. crotonensis* the introduction of HCB caused a decrease in growth rate, μ. In two typical experiments (Fig. 1) μ declined by 30−40% within 2 d after the addition of HCB. (A slight increase in μ was observed preceding the decline in two experiments, but not in others.) When μ started to decline, the cellular HCB concentration was about 11×10^{-8} to 15×10^{-8} ng/cell, or 2.1−2.9 μg/g dry weight. After this initial decrease there was a further decline, accompanied by an increase in cellular HCB. In some experiments, on the 8th d of HCB flow the HCB medium in the reservoir was replaced with HCB-free medium. In all cases there was an immediate increase in μ, accompanied by an exponential decrease in cellular HCB; μ increased far above the rate without HCB and then returned to the original steady-state rate. The decrease of cellular HCB in the other culture in Fig. 1 was due not to the removal of HCB, but to a low HCB concentration in the new batch of the reservoir medium.

Cellular HCB in *F. crotonensis* during HCB flow plotted against μ for all experiments indicates a dose−response relationship (Fig. 2). Because of the scatter of data points, it is not clear whether the relationship is linear or curvilinear with a sharp decline in μ at low concentrations. It is also possible that there is a threshold concentration below which toxic effects are not manifested. At any rate, a *t*-test of the grouped data of μ shows that the means of μ with and without HCB were significantly different at the 5% level. The slope of

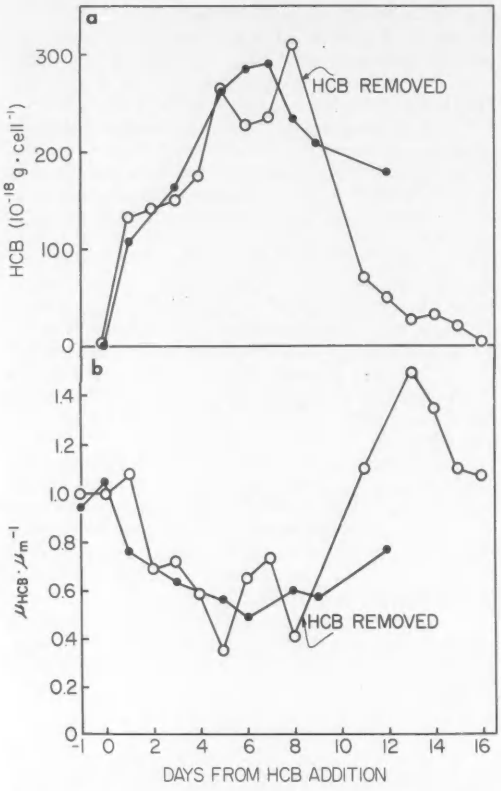

FIG. 1. Time course of changes in (a) cellular HCB concentrations and (b) growth rate for two nutrient-sufficient *Fragilaria crotonensis* cultures. For one culture (○) the HCB medium in the reservoir was replaced with HCB-free medium on the 8th d of HCB flow; in the other (●) the decrease of cell HCB was due to a low HCB concentration in new medium in the reservoir. Growth rate is expressed as the rate after the addition of HCB relative to the maximum growth rate in HCB-free medium (μ_{HCB}/μ_m); μ_m was 0.78/d.

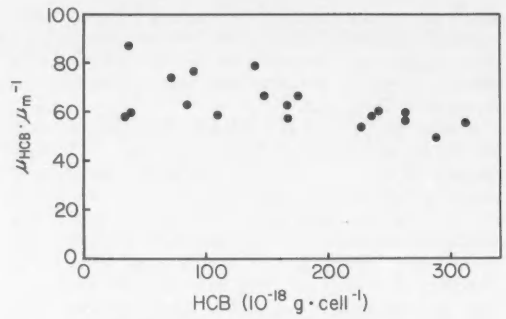

FIG. 2. Pooled data for dose–response relationship in *Fragilaria crotonensis* between μ_{HCB}/μ_m and cell HCB concentrations. The relative growth rate was taken from the 2nd d after the addition of HCB until the end of experiment or until HCB medium in the reservoir was replaced with HCB-free medium.

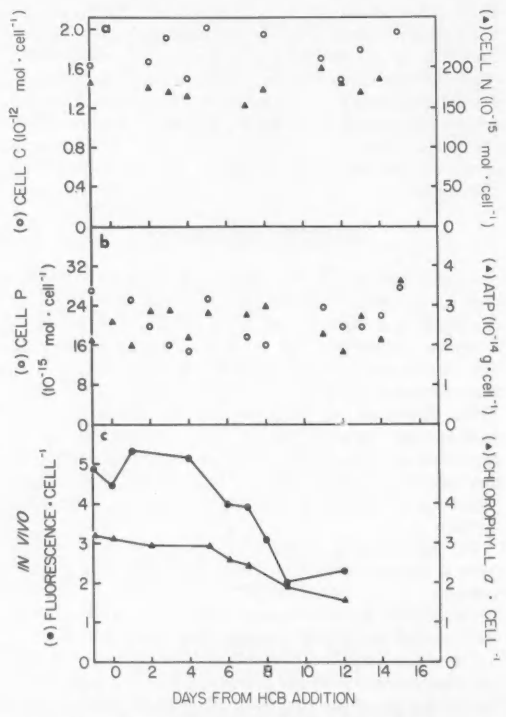

FIG. 3. Time course of changes in cellular composition in nutrient-sufficient *Fragilaria crotonensis*: (a) cell C (○) and cell N (▲), (b) cell P (○) and cell ATP (▲), and (c) chlorophyll *a* measured by extraction method (▲) and by in vivo fluorescence (●). The data are the results from two cultures.

regression of the μ_{HCB}/μ_m, the growth rate of cultures with HCB relative to that of HCB-free cultures, was also significant at 5% (*t*-test), suggesting a dose–response relationship. The relationship in Fig. 2 does not hold for the responses during dilution or for the relaxation of cellular HCB after HCB is removed from the reservoir medium. During this period the culture exhibited an "overshooting" of μ and a rapid decrease in cellular HCB.

With the addition of HCB, cellular chlorophyll *a* concentrations also decreased in nutrient-sufficient *F. crotonensis* (Fig. 3). The decrease appears to be parallel with the reduction in μ and the gain in cellular HCB. There is considerable scatter in cellular P, N, and ATP concentrations (Fig. 3), and they do not seem to change significantly.

The ^{14}C fixation rate per cell (an average of 3.54×10^{-10} μmol · cell^{-1} · min^{-1}) did not vary with the addition of HCB, but cellular chl *a* concentration decreased. Therefore, assimilation rate of C (C fixed · chl a^{-1} · time^{-1}) increases with the accumulation of HCB.

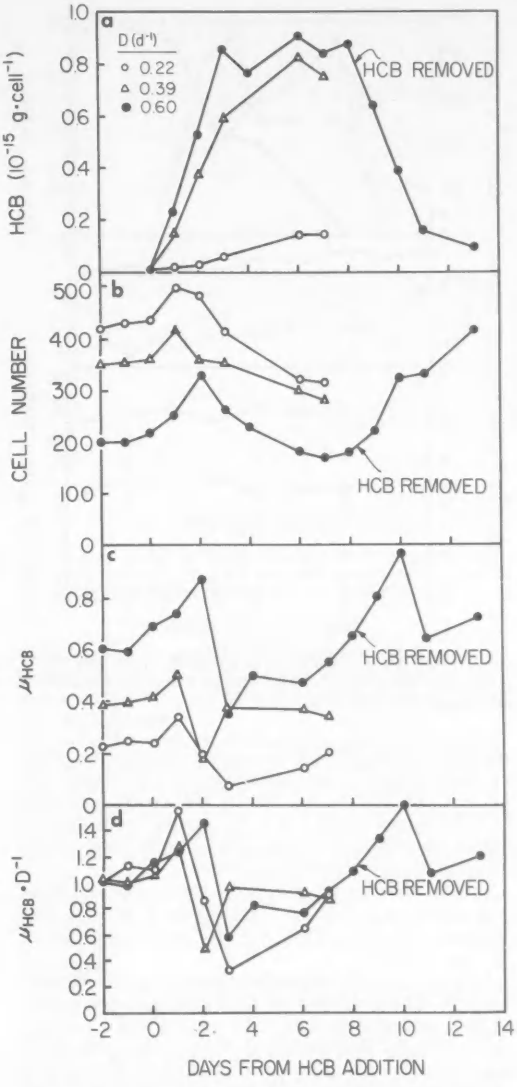

FIG. 4. Time course of changes in cell HCB concentrations, cell number, and growth rate in P-limited *Fragilaria crotonensis* in a chemostat: (a) cell HCB concentrations, (b) cell number, (c) growth rate (μ_{HCB}), and (d) relative growth rate (μ_{HCB}/μ_m).

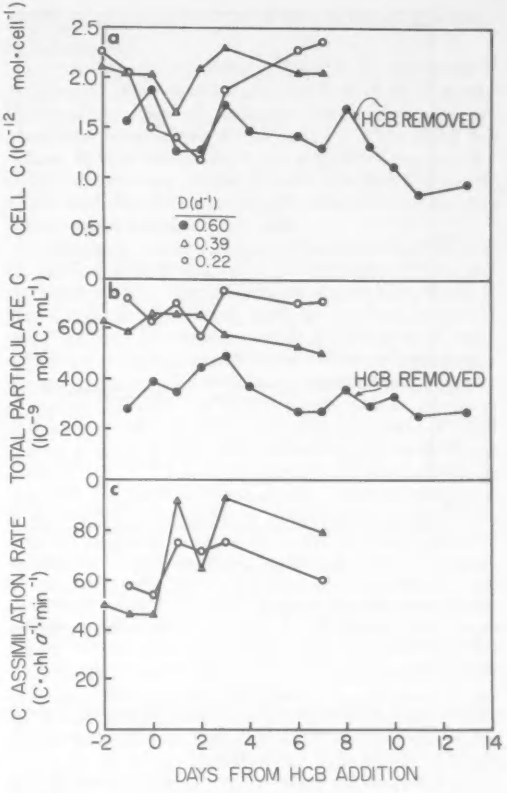

FIG. 5. Time course of changes in (a) cell C, (b) total particulate C per culture volume, and (c) ^{14}C assimilation rate in P-limited *Fragilaria crotonensis*.

To ascertain the effects of HCB under P limitation, a condition which occurs in most freshwater environments, *F. crotonensis* were run at three dilution rates (D) in a P-limited chemostat representing various degrees of P limitation (see Rhee 1980): 0.22, 0.39, and 0.60/d (Fig. 4). In these cultures a change in cell number represents a change in μ (see Equation (1)). It soon became apparent, however, that it was extremely difficult to control cellular HCB concentrations in these experiments because (i) culture density was higher at lower D and (ii) more HCB adsorbed to the medium flow line from the reservoir at lower values of D due to longer residence time in the line. Thus, no dosage comparison could be made between different values of D.

Despite considerable differences in cellular HCB concentrations, there was a marked increase in cell numbers within 2 d after HCB flow at all Ds, which is followed by a decrease to levels below those in HCB-free medium (Fig. 4). These responses are dissimilar to those observed in nutrient-sufficient cultures, where there was only a slight gain or no gain in μ. In one of the cultures (0.60/d) the HCB medium in the reservoir was replaced with HCB-free medium after 8 d of HCB flow. The cell numbers, thus μ, first increased far above the level in HCB-free medium and then returned to the original steady-state level attained before HCB addition. This overshooting is similar to that observed in nutrient-sufficient cultures.

At all dilution rates, or degrees of P limitation, the pattern and extent of supression in the relative growth rate (μ_{HCB}/μ, μ in HCB-containing cultures relative to that in HCB-free

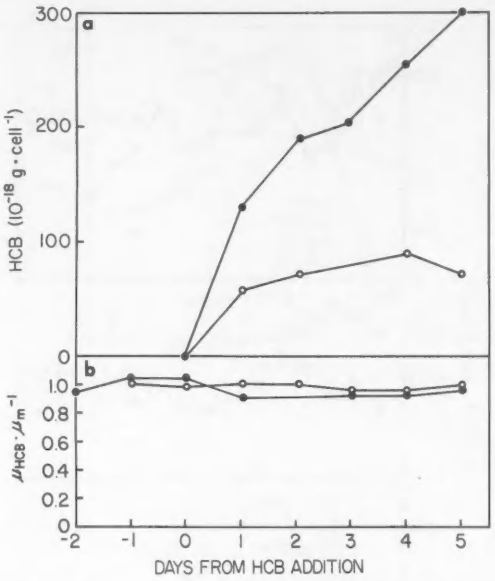

FIG. 6. Time course of changes in (a) cell HCB and (b) relative growth rate (μ_{HCB}/μ_m) in two cultures of *Ankistrodesmus falcatus* under nutrient-sufficient conditions; the maximum growth rate μ_m was 0.97/d.

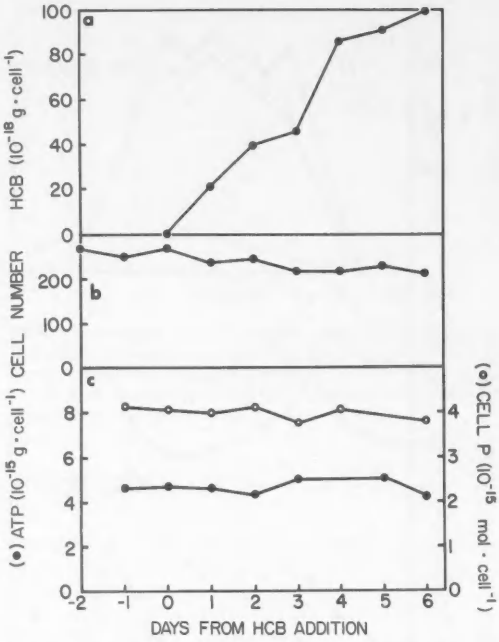

FIG. 7. Time course of changes in (a) cell HCB, (b) cell number, and (c) cell ATP (●) and cell P (○) in P-limited *Ankistrodesmus falcatus*; the dilution rate was 0.17/d.

cultures) were similar. However, neither the relative growth rate nor growth rate during HCB flow (μ_{HCB}) appears to be related to cellular HCB levels (Fig. 4).

It was not possible to find a dose–response relationship at each dilution rate in the chemostat cultures, mainly due to the insufficient number of data points. It is clear, however, that if a relationship existed, it would be different from the one in nutrient-sufficient cultures, as μ was enhanced with the start of HCB addition in chemostats.

Despite the changes in culture density in P-limited chemostat cultures of *F. crotonensis*, cellular C per unit culture volume remained relatively constant through each experiment. Therefore the increase in μ immediately following HCB introduction was due to increased rate of cell division without a concomitant increase in C fixation, resulting in a decrease in cellular C concentrations (Fig. 5). Similarly the increase of cell number when HCB was removed was accompanied by a decrease in cell C. As in nutrient-sufficient cells, however, the assimilation rate increased with the bioaccumulation of HCB (Fig. 5).

Cellular P also decreased from $5.8 \times 10^{-15} \pm 0.006 \times 10^{-15}$ to $4.8 \times 10^{-15} \pm 0.20 \times 10^{-15}$ mol/cell as cell division was stimulated with the inflow of HCB and remained at a low concentration. It decreased further with the removal of HCB from the reservoir which resulted in an increased cell division rate. These results deviate from the relationship between μ and intracellular nutrient concentrations in the intracellular pool models for nutrient-limited growth (see Rhee 1980).

The nutrient-sufficient cultures of *A. falcatus* showed no inhibitory effects of HCB at cellular concentrations comparable to those in *F. crotonensis* (Fig. 6). Cell P and ATP did not vary during the experimental period, averaging 18×10^{-9} μmol P and 1.0×10^{-5} ng ATP/cell. The ^{14}C fixation rate (0.4×10^{-9} μmol C · cell^{-1} · min^{-1}) and cellular chlorophyll *a* also remained unaffected.

Under P limitation ($D = 0.17$/d), there was also no inhibitory effects on μ (Fig. 7). Total cellular P and ATP also appeared constant at about 4×10^{-6} ng/cell and 0.48×10^{-5} ng ATP/cell.

Microcystis sp. also showed no change in μ with the addition of HCB under nutrient-sufficient conditions up to a cellular HCB concentration of 48×10^{-9} ng/cell or 3.4 μg/g dry weight (Fig. 8). Replacement of HCB medium with HCB-free medium in the reservoir did not affect μ. Although the concentration of cellular HCB was lower in *Microcystis* sp. than in either *F. crotonensis* or *A. falcatus*, on a dry weight or cell volume basis the HCB concentration was comparable to those in the two other species. Cellular C and P also did not vary with the addition of HCB, averaging 5×10^{-7} μmol C and 7.2×10^{-9} μmol P/cell. There was also no change in chl *a* concentrations.

Discussion

It is most interesting to find a general dose–response relationship between intracellular HCB concentrations and μ during HCB flow in nutrient-rich *F. crotonensis* (Fig. 2).

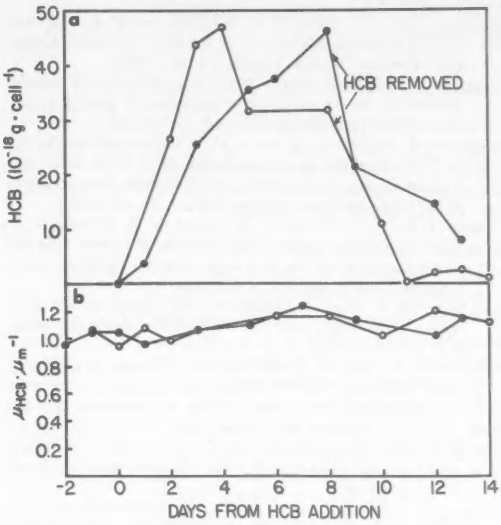

FIG. 8. Time course of changes in (a) cell HCB and (b) relative growth rate (μ_{HCB}/μ_m) for two nutrient-sufficient cultures of *Microcystis* sp.; μ_m was 0.90/d.

Although it is not possible to characterize the relationship further with only the small number of data points at hand, such a relationship could be used as the basis for a bioassay for toxic chemicals.

Because the bioconcentration factor and bioaccumulation vary with population density (see references in the introduction), it may then be expected that the manifestation of toxicity is influenced by the density. Indeed, it has been reported that the effects of PCBs on photosynthesis of *Chlorella* are more severe in dilute cell suspensions with the same amount of PCBs per volume of culture (Cole and Plapp 1974). It is therefore important to relate toxic or inhibitory effects to the intracellular level of toxicants. This enables us to compare different studies, as well as different experiments in the same investigation.

In the present study it was extremely difficult to control in advance the concentrations of HCB in the culture medium. Among the difficulties is the loss by adsorption to culture apparatus, volatilization, and codistillation with water; as much as 70% of the reservoir HCB was lost by the time the medium reached the culture vessel. Furthermore, this loss varied with the retention time of the culture (or the flow rate of medium). These problems also contributed to the difficulties of controlling cellular HCB concentrations.

It was also difficult to determine accurately external HCB concentrations because of the low specific activity of the isomer (2.12 MBq/μmol). In general the concentrations of dissolved HCB in the medium were less than 20 ng/L. These concentrations are comparable to those in Saginaw Bay, Lake Huron, where soluble PCB concentrations are 12–24 μg/L (W. L. Richardson, U.S. EPA, Grosse Ile, MI, personal communication). In terms of dry weight, however, the total HCB in the biomass of our culture was about an order of magnitude higher than the total PCBs in the particulate matter in Saginaw Bay.

Growth rate was stimulated in P-limited *F. crotonensis* at all dilution rates within 2 d after the flow of HCB started. However, we could not determine whether there was any correlation between growth (cell division) enhancement and cellular HCB or whether there was a threshold concentration of HCB for inhibitory effects. As cultures at each dilution rate represented different physiological states, only a few data points were available for each state.

Although the overall responses of the turbidostat cultures to the addition of HCB were alike, it is difficult to explain why the initial reactions were different between cultures shown in Fig. 1. It is also not clear why there were marked increases in μ in P-limited *F. crotonensis* with the addition of HCB, while only a few of the nutrient-sufficient cultures showed even a sight enhancement. These differences between the responses of nutrient-sufficient and P-limited cells may be related to differences in cell composition. Besides differences in cell P content (Fig. 3, 6) there were noticeable differences in cell lipid: 30.6×10^{-6} μg/cell for nutrient-sufficient cells versus 3.9×10^{-6} μg/cell for P-limited cells. However, differences in the distribution of lipids in various cellular components were not measured. It is most likely that inhibitory effects of toxicants are related to their concentration within individual cell fractions, rather than to the total amount associated with a cell. For example, PCBs associated with active membranes would probably be more toxic than PCBs in lipid storage pools.

Of the three species tested, only *F. crotonensis* showed inhibitory effects of HCB on growth rate. *Microcystis* sp. and *A. falcatus* exhibited no such effects at comparable cellular and external concentrations of HCB. On a dry-weight basis, the HCB concentration was higher in *A. falcatus* and *Microcystis* than in *F. crotonensis*. There was no correlation between inhibitory effects and bioconcentration factors among species. The bioconcentration factor was highest in *A. falcatus* and lower in *Microcystis* and *F. crotonensis*. These values were comparable in magnitude whether calculated on the basis of cell number, dry weight, cellular C, or lipids (Lederman and Rhee 1982). Interspecific differences in toxic effects have also been found by Fisher et al. (1974). Therefore it appears that environmental contamination with PCBs can alter community composition, with the potential consequence of disrupting the balance of an ecosystem.

Adknowledgments

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Ecological Studies of Arctic Cod (*Boreogadus saida*) in Beaufort Sea Coastal Waters, Alaska

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CRAIG, P. C., W. B. GRIFFITHS, L. HALDORSON, AND H. MCELDERRY. 1982. Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. Can. J. Fish. Aquat. Sci. 39: 395–406.

Fish use of Beaufort Sea coastal waters was examined during summer and winter periods 1977–80. Arctic cod (*Boreogadus saida*) were abundant but their occurrence was highly variable. They accounted for 8–78% of all fish caught in Simpson Lagoon during two summers, and 0.4–100% of catches at various coastal sites in winter. Arctic cod increased in abundance in the lagoon during late summer and some association was noted between their numbers and higher salinities but not temperature or turbidity. Some cod remained in shallow waters in early winter but deeper areas were used through the winter, and the highest catch rate was recorded 175 km offshore. Principal foods of the cod in nearshore waters were mysids (*Mysis litoralis*, *M. relicta*), amphipods (*Onisimus glacialis*), and copepods. The cod caught were generally small (60–170 mm) and young (ages 1–3). Most males matured at ages 2–3 and females at age 3. These size, age, and maturity characteristics indicate a life history strategy (*r*-selection) unlike that typified by many other arctic fish populations, particularly the freshwater and anadromous species which tend to be slow growing, late maturing and long-lived (*K*-selection).

Key words: Arctic cod, *Boreogadus saida*; Beaufort Sea, distribution, life history strategy

CRAIG, P. C., W. B. GRIFFITHS, L. HALDORSON, AND H. MCELDERRY. 1982. Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. Can. J. Fish. Aquat. Sci. 39: 395–406.

Nous avons étudié, pendant les étés et les hivers de 1977 à 1980, l'usage que l'on fait du poisson des eaux côtières de la mer de Beaufort. Le saida (*Boreogadus saida*) est abondant mais d'occurrence très variable. Cette espèce représente 8–78 % de tous les poissons capturés dans la lagune Simpson pendant deux étés et 0,4–100 % des prises à divers sites côtiers en hiver. L'abondance du saida dans la lagune augmente à la fin de l'été et nous avons noté une certaine association entre leurs nombres et des salinités élevées, mais non la température et la turbidité. Quelques saida demeurent en eau peu profonde au début de l'hiver, mais, durant cette saison, ils se trouvent en eau plus profonde, et les taux de capture les plus élevés sont signalés à 175 km au large. Les principaux organismes ingérés par le saida dans les eaux côtières sont des mysides (*Mysis litoralis*, *M. relicta*), des amphipodes (*Onisimus glacialis*) et des copépodes. Les saida capturés sont généralement petits (60–170 mm) et jeunes (âges 1–3). La plupart des mâles atteignent la maturité aux âges de 2 à 3 et les femelles à l'âge 3. Ces caractéristiques de taille, d'âge et de maturité indiquent une stratégie de cycle biologique (sélection r) différente de celle des autres populations de poissons arctiques, en particulier les espèces anadromes dulçaquicoles qui tendent à croître lentement, à atteindre la maturité tard et à vivre longtemps (sélection *K*).

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ARCTIC cod (*Boreogadus saida*) has been described as a "key species in the ecosystem of the Arctic ocean" because of its abundance, widespread distribution, and importance in the diets of marine mammals, birds, and other fish (e.g. Andriyashev 1954; Quast 1974; Bain and Sekerak 1978). Several authors have suggested that Arctic cod influences the distributions and movements of marine mammals and seabirds in arctic waters (Klumov 1937; Bradstreet 1980; Davis et al. 1980; Finley and Gibb 1982). Despite recognition of its ecological significance, the biology of Arctic cod in Beaufort Sea waters (and elsewhere) is not well known. Some data are available (Bendock 1977; Lowry and Frost 1981), but much of our knowledge is derived from the Soviet literature, and, more recently, from studies conducted in the Canadian High Arctic (Bain and Sekerak 1978; Sekerak 1982) and the northern Atlantic Ocean (e.g. Lear 1979). This lack of information reflects a research emphasis over the past decade on data

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related to freshwater and anadromous species directly affected by initial industrial developments in the Arctic. In recent years, however, some attention has focused on marine species not only as oil exploration extends into coastal waters, but also in response to requests from other biological disciplines needing information about important prey species, particularly the Arctic cod (OCSEAP 1978).

A need for more information about Arctic cod is apparent, especially because this single species constitutes a major trophic link between zooplankters and upper trophic levels (including man) of the arctic ecosystem. The present study was undertaken to examine fish populations and their year-round utilization of coastal waters of the Beaufort Sea. Arctic cod was a major species in the study area and also one of the few species utilizing coastal habitats during both summer and winter periods.

Study Area

Summer studies were conducted in the brackish waters of Simpson Lagoon, located between Prudhoe Bay and the Colville River delta on Alaska's North Slope (Fig. 1). The lagoon is a large and partially enclosed body of water measuring ~35 km in length and 3–6 km in width. It is a shallow-water basin with an average depth of only 2 m (maximum 3 m). The lagoon floor is uniformly flat and almost featureless. In most areas, a layer of detritus covers substrates of mud and sand.

The ice-free period in the lagoon is short, lasting about 3 mo (early July to early October). Summer salinities (1–32‰) and temperatures (0–14°C) fluctuate as a direct influence of the prevailing westward flowing Beaufort Sea current, wind, and freshwater runoff. Lagoon waters are diluted by freshwater runoff and are correspondingly lower in salinity (4–5‰) and higher in temperature (2–4°C) than waters immediately seaward of the barrier islands. This difference is not as marked late in summer as runoff declines. Prevailing currents continually exchange lagoon water at an average rate of 10–20%/d, and 100%/d when aided by exceptionally strong winds (65 km/h) (Mungall 1978). During the winter, exchange diminishes substantially as surface ice steadily increases in thickness to about 2 m. By late winter (April) ~90% of the lagoon volume is frozen solid. Hypersaline conditions (up to 68‰, Crane 1974) develop from salt exclusion during ice formation.

Winter studies were conducted in Simpson Lagoon as well as other nearshore and offshore locations between the Colville and Sagavanirktok rivers (Fig. 1). Under-ice water depths at these sites were 1–12 m except at one station 175 km offshore where the water depth was 2500+ m.

Additional details about the study area appear in Craig and Haldorson (1981) and Griffiths and Dillinger (1981).

Methods

Summer Programs

During the open-water seasons of 1977 and 1978, fish were sampled by seine, gillnet and fyke net, but Arctic cod were caught efficiently only by fyke net (catch results by species and gear type are provided in Craig and Haldorson (1981)).

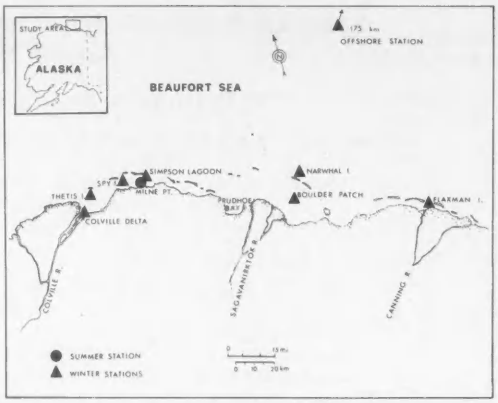

FIG. 1. Locations of the summer sampling site at Milne Point in Simpson Lagoon, and winter sites at various nearshore and offshore locations.

The fyke net was set perpendicular to the shoreline with the lead net attached to shore. Mesh sizes (stretched) were 1.2 cm for the trap and 2.5 cm for wing and lead nets. In 1977, the lead net measured 33.3 m long and wing nets were 7.6 m. In 1978, these dimensions were doubled, net color was changed from green to gray, and two traps were used simultaneously so that the direction of fish movements could be determined; however, directional trends for Arctic cod were not apparent so numbers of cod in the two traps were combined for data analysis. The larger 1978 fyke net appeared to be a more suitable sampling device than the 1977 version; on one memorable occasion, a single trap held over 25 000 Arctic cod (60–140 mm in length) with no observable fish mortality. All fish caught were counted, although during peak catches of Arctic cod, numbers were estimated by counting the number of Arctic cod in a dip net filled to a given level, repeating this for several additional samples, and then applying the mean number per netful to the total number of netfuls in the trap. Subsamples were measured.

A modified Faber net (Faber 1968) with a 0.5-m diameter and 1.0-mm mesh was used to sample planktonic fish in 1977. Three sites inside Simpson Lagoon and one site immediately outside the lagoon were sampled at about 10-d intervals from July 11 to September 14. On each date two replicate, horizontal tows were made at each site, weather and ice permitting. Each tow filtered ~83 m^3 of surface water (i.e. a 5-min tow at 1.4 m/s).

Winter Programs

Under-ice sampling programs were conducted during three winters. Sites included the Colville Delta (April–May 1978), several nearshore sites between the Colville Delta and Narwhal Island (November 1978, February, March, April and November 1979, May 1980), and one offshore site located 175 km north of Prudhoe Bay (May 1980). A Global Navigation System 500 and VHF homing device were used to relocate the offshore station at 71°49.7′ N, 148°22.6′ W.

Difficulties in collecting fish in ice-covered areas necessi-

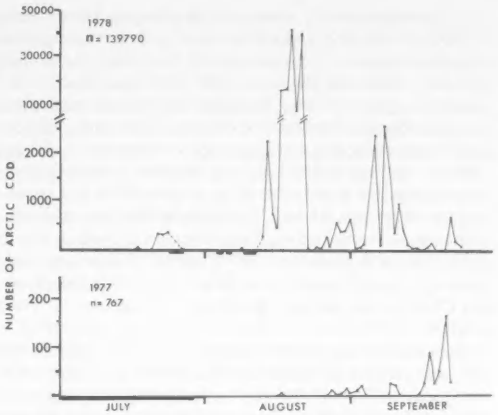

FIG. 2. Daily catch of Arctic cod at Milne Point, Simpson Lagoon. Dark bars along abcissa indicate periods when the fyke net did not operate.

tated the use of a variety of nets during winter studies. Gillnets (47.2 m long with various combinations of stretched mesh sizes ranging from 1.9 to 8.9 cm) and fyke nets (with four 27.4-m lead nets and common trap) were the principal gear used. Nets were set at or near the bottom of the water column to avoid freezing to the under-ice surface except at the deep offshore station where the fyke net was set directly under the ice (this station was sampled in late winter when ice growth was essentially complete). Details of net types and time fished are presented in Craig and Haldorson (1981). The overall winter sampling effort in coastal waters was extensive.

Gear	Days fished
Gillnets	252
Fyke nets	62
Minnow traps	14
Trammel nets	10
Box trap	1

An under-ice plankton net was used to collect pelagic eggs and larvae of arctic cod. The 2-m-diameter net (0.5-mm mesh) was collapsible in order to fit through a 20-cm hole in the ice. Three replicate, vertical tows were made at each sample site.

Laboratory Analysis of Fish

Laboratory analysis of fresh fish included determination of fork length to the nearest millimetre, weight to the nearest gram, sex, maturity, and age (otoliths). Maturity was judged from a field evaluation of reproductive condition, aided by measurements of egg sizes or testes weights. Fish stomachs were preserved separately in Formalin and later analyzed in the laboratory. Because the variety of food items in stomach contents of individual fish was low and the relative proportions of major food groups did not vary greatly, a sample of only 10–20 stomachs from each sampling period appeared adequate to describe the kinds and proportions of important food items consumed (Craig and Haldorson 1981); actual numbers of stomachs examined per sampling period were 20–84. A Mettler PL200 balance was used to determine Formalin-preserved wet weights of identifiable items. Unidentifiable materials were not included in calculations or percent composition.

Invertebrate Samples

Because fish in the study area ate primarily mobile epibenthic invertebrates, a central pursing drop net was designed by modifying an epibenthic sampler developed by Clutter (1965). The net diameter was 0.5 m, height was 0.75 m, and mesh size was 1.0 mm. With both top and bottom ends of the net open, it was thrust by pole to the bottom in shallow water; in deep water the net was weighted to free-fall. Upon reaching the sea bottom, purse lines to top and bottom net openings were immediately pulled to enclose the sample in the net. Five replicate samples were collected at each site of fish capture. Further details are provided by Griffiths and Dillinger (1981).

Physical and Chemical Measurements

Water temperature and salinity (Hydrolab model TC-2) and turbidity (DRT-15 Turbidimeter, H. F. Instruments) were measured daily 80 m from shore at Milne Point, Simpson Lagoon, where the fyke net was operated.

Results

Relative Abundance

During the 3-mo open-water season, brackish nearshore waters along the Beaufort Sea coastline are used extensively by anadromous and marine fishes for feeding. Over 28 species have been recorded (Craig and McCart 1976), but a few marine fishes (Arctic cod, fourhorn sculpin (*Myoxocephalus quadricornis*)) and anadromous fishes (Arctic char (*Salvelinus alpinus*), Arctic cisco (*Coregonus antumnalis*), least cisco (*C. sardinella*)) generally account for 90% of the nearshore fish community (OCSEAP 1978).

Numbers of Arctic cod in Simpson Lagoon varied greatly during the two summers of study. In 1977 relatively few cod were caught and they accounted for only 8% of the total fyke net catch (767 of 10 026 fish). The following summer, large numbers of Arctic cod (estimated in the millions) entered Simpson Lagoon; the actual 1978 catch of 139 790 Arctic cod was ~ 14 times larger than the total number of fish (all species combined) caught during the previous summer. In fact, on four separate dates in 1978, the daily catch of Arctic cod exceeded the total 1977 catch of all species. Between-year differences in sampling methods undoubtedly affected the size and species composition of the catch; however, the almost 200-fold increase in numbers of Arctic cod caught in 1978, and their overwhelming dominance of the 1978 species composition in fyke net catches from the lagoon (from 8% in 1977 to 78% in 1978), demonstrate that fish numbers and relative abundance in the lagoon–barrier island ecosystem may fluctuate dramatically from year to year.

Young-of-year (yoy) Arctic cod were also abundant in

summer. In 1977, they accounted for 83% of the 366 larval fish caught in the lagoon. Densities were highly variable, ranging from 0 to 855 yoy/dam^3, with a summer average of 78 yoy/dam^3 (n = 23 pairs of net samples, SD = 222). The following summer, yoy cod were apparently less abundant; a subsample of 52 yoy fish consisted of 25% gadids, 61% cottids, and 14% liparids. (Note: 1 dam^3 = 1000 m^3.)

In winter, juvenile and adult Arctic cod were again the predominant species at most winter sampling stations. They accounted for 100% of all fish caught at the 175-km-offshore site (n = 65), 100% at Narwhal Island (n = 9), 80% at the Boulder Patch in Stefansson Sound (78 of 97), 56% at Flaxman Island (9 of 16), and 37% at Simpson Lagoon (26 of 70). In contrast, no cod were taken in the brackish waters within the Colville Delta (n = 150, mostly Arctic and least cisco) and few were taken in nearshore waters near the Colville River; at Thetis Island, only 0.4% of the catch was Arctic cod (n = 2612, mostly boreal smelt (*Osmerus eperlanus*) and fourhorn sculpin).

Distribution and Movements

Although the distribution of Arctic cod is often associated with the occurrence of ice (Andriyashev 1954), catch data show that these fish are present in ice-free nearshore waters. Many young-of-year were collected in the study area during summer and their distribution is widespread because young-of-year were abundant at other nearshore sites along the north coast of Alaska (Bendock 1977; Griffiths et al. 1977) and also 50–150 km offshore in the Beaufort and Chukchi seas (Quast 1974; OCSEAP 1978; Hunter 1979).

Older cod were abundant in Simpson Lagoon, particularly during the latter part of the open-water season (Fig. 2). Cod were present for a prolonged period, but in addition a massive school of cod swept through the lagoon in mid-August of 1978. During a 9-d period (August 14–22), ~124 200 Arctic cod were caught in the Milne Point fyke net. The fish were highly mobile as indicated by erratic daily catches; for example, approximate daily catches during August 18–22 were 17 000, 42 000, 6000, 40 000, and 15. There was no clear directional pattern of movements at this time. These were generally small and young fish (60–160 mm, which corresponds to ages 1–3). The Arctic cod run was not restricted to Simpson Lagoon, but was also observed elsewhere along the Beaufort Sea coastline; a large school of Arctic cod measuring ~35 m wide and 300 m long was observed travelling along the shoreline in Prudhoe Bay in August 1978 (C. Broad, Western Washington Univ., Bellingham, WA, personal communication). Arctic cod were also common in Prudhoe Bay in 1975 and 1976 (Bendock 1977) and they were the most numerous species caught in offshore waters of the northeastern Chukchi and western Beaufort seas (Lowry and Frost 1981).

Some cod remained in Simpson Lagoon in early winter (November), but all appeared to vacate these shallow waters by February (Table 1). Nearby deeper coastal waters between the Colville and Canning rivers were inhabited by cod through the winter, but the catch per unit effort (CPUE) was highest offshore; in the late winter collection period, when a single type of sampling gear (under-ice fyke net) was used, the CPUE was over 30 times greater 175 km offshore than in the Boulder Patch in Stefansson Sound.

The above distributional information must be interpreted with some discretion because the data reflect, in part, the type of sampling gear used to collect the fish. Because of their shape, Arctic cod in our area are usually difficult to capture in gillnets. For example, only a single Arctic cod was caught in 44 gillnet sets during the 1977 open-water season in Simpson Lagoon whereas a fyke net caught 767 during the same period. It is probably due to this same gear selectivity that the Arctic cod has not been reported as an abundant species along the Alaskan and Yukon coastlines as most earlier studies relied upon gillnets as a primary sampling technique. However, by November the body shape of Arctic cod changes somewhat due to advanced gonadal development and full stomachs, and so some become susceptible to capture by

TABLE 1. Winter catch per unit effort (CPUE) for Arctic cod at various coastal locations. Gillnet and fyke net data are combined and total sampling effort in days is listed in parentheses.

	CPUE (fish/day)						
Date	Thetis Island	Spy Island	Simpson Lagoon	Boulder Patch	Narwhal Island	Flaxman Island	175 km offshore
Early winter							
Nov. 13–16, 1978	0.5(12)	—	0.9(24)	0.7(18)	0.5(1)	—	—
Nov. 4–15, 1979	2.0(2)	—	0.3(20)	0.3(15)	—	4.5(2)	—
Average	0.7	—	0.6	0.5	0.5	4.5	—
Midwinter							
Feb. 11–27, 1979	0(20)	—	0(7)	3.7(14)	0(16)	—	—
Late winter							
Mar. 1–Apr. 1, 1979	0(52)	—	—	—	—	—	—
Apr. 29–May 14, 1979	0(13)	0(10)	0(10)	0.4(17)	0.5(15)	—	—
Apr. 29–May 6, 1980	—	—	—	0.3(7)	—	—	10.8(6)
Average	0	0	0	0.4	0.5	—	10.8
Approx. late-winter water depth (m)	1.7	3.3	0.5	4.6	10.0	0.5	2500+

gillnet. After spawning in midwinter, cod were again caught only by fyke net. Because variable combinations of gillnets and experimental under-ice fyke nets were used during our winter sampling trips, the catch-per-unit-effort data in Table 1 are not directly comparable. In particular, the relatively high midwinter catch at the Boulder Patch in Stefansson Sound is probably due to the use of fyke nets there and gillnets elsewhere. Data were combined in Table 1 because a variety of nets were used as the program progressed and new modifications were continually tested.

Abundance in Relation to Temperature, Salinity, and Turbidity

An apparent preference of Arctic cod for low water temperatures has been noted by Russian researchers (Andriyashev 1954; Nikolskii 1954), and the Simpson Lagoon data are consistent with this. During both summers of study, occasional Arctic cod visited Simpson Lagoon between mid-July and mid-August when waters were relatively warm (typically 6−10°C) and salinities were low (typically 10−20‰), but it was not until after mid-August when water temperatures were dropping and salinities were increasing that Arctic cod numbers increased. Typical shoreline water temperatures and salinities during this latter period were 0−6°C and 20−30‰.

Despite this overall trend, Arctic cod were tolerant of the widely fluctuating temperatures, salinities, and turbidities common in Simpson Lagoon during the open-water season. For at least short periods of time, the fish were able to cope with conditions ranging from nearly fresh to saltwater (3−28‰), clear to very turbid water (1−146 NTU), and temperatures ranging from 0 to 13.5°C. These ranges represent the values on days when cod were caught by fyke net in Simpson Lagoon.

Because daily catches of Arctic cod were highly variable, numbers caught were compared with daily fluctuations in water temperature, salinity, and turbidity at Milne Point during the summer of 1978. To minimize effects of seasonal movements of fish and seasonal changes in physical factors, the open-water season was divided into four time periods for separate analyses: July 10−19 (n = 6 observations during this period when all appropriate data were available), July 20−August 10 (n = 12), August 11−31 (n = 13), September 1−20 (n = 16). General changes in temperature and salinity provided some basis for the selection of these four periods. Actual ranges of physical variables and numbers of Arctic cod during these periods were, in order:

Period	Temp. (°C)	Salinity (‰)	Turbidity (NTU)	No. Arctic cod
1	5−7	1−18	40−87	18
2	4−13.5	9−28	3−47	751
3	2−7	14−26	4−36	125 590
4	0.5−5	13−29	2−98	9 163

Because each day's fish catch covered a 24-h period, daily catches of each species were compared with average values for physical data collected at the start and end of each corresponding 24-h period.

Only one of the 12 correlation coefficients (three variables × four time periods) was statistically significant; daily catches of arctic cod showed a positive correlation with salinity during the fourth period (r = 0.655, $P < 0.01$). When statistical probabilities (both significant and not significant) obtained for each variable during the four time periods were pooled using the "weighted z" test (Rosenthal 1978), only the correlation between salinity and number of arctic cod was significant (z-pooled, one-sided P = 0.02). These results suggest that some of the observed variation in daily catches of cod may be influenced by salinity conditions in nearshore waters. Hydroacoustic studies in Prudhoe Bay indicate that Arctic cod may be associated with the leading edge of the marine water mass which moves back and forth almost daily in a seaward/landward direction in shallow coastal waters (L. Moulton, Alaska Dept. Fish and Game, Anchorage, AK, personal communication).

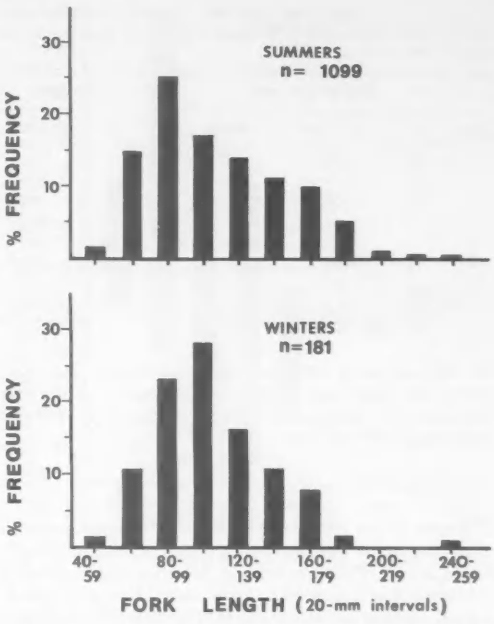

FIG. 3. Length frequencies of Arctic cod (excluding young-of-year) caught in Simpson Lagoon in summer (July−September 1977 and 1978) and in nearshore waters between Thetis and Narwhal islands in winter (November−May 1978−79 and 1979−80).

Size Distribution

Arctic cod caught in Simpson Lagoon and surrounding nearshore waters in summer ranged in fork length from 6 to 60 mm (usually 7 to 21 mm) for young-of-year and from 45 to 257 mm (usually 60 to 170 mm) for older fish. Sizes of older cod caught during the open-water and winter periods were similar (Fig. 3).

The sizes of older Arctic cod in Simpson Lagoon are similar to those recorded in Prudhoe Bay in 1975 and 1976 (Bendock 1977) but are considerably larger than the size distribution

TABLE 2. Age–length relationship and sex ratio of combined samples of Arctic cod caught in Simpson Lagoon and adjacent coastal waters, 1977–80.

	Fork length (mm)			Sex ratio	
Age	*n*	$\bar{x} \pm$ SD	Range	*n*	% female
1	225	84±13	54–110	—	—
2	137	128±20	88–177	111	57
3	94	159±21	120–196	91	70
4	19	180±20	129–203	18	83
5	9	209±34	153–250	8	88
6	4	240±28	198–257	4	75
Total	488			232	66

of cod caught in offshore waters by Lowry and Frost (1981). Most of the offshore cod, which were caught by otter trawl in water depths of 40–400 m, measured 60–110 mm (total range 45–180 mm).

AGE AND GROWTH

Young-of-year Arctic cod were caught in Faber trawls in Simpson Lagoon and in marine waters seaward of Pingok Island in 1977. Early catches (July 21) in the lagoon averaged 7.8 mm in length (range 6–11 mm, $n = 12$ preserved specimens), whereas late season catches (September 14) averaged 19.0 mm (range 12–29, $n = 17$ preserved specimens). On one occasion when young-of-year were collected both inside Simpson Lagoon and 2 km offshore in slightly colder marine waters (September 14, 2.5°C vs. 0.5°C), there was no significant difference (t-test) in the size of the fish (Simpson Lagoon, $\bar{x} = 18.1 \pm 4.2$ ($n = 12$); offshore, $\bar{x} = 21.2 \pm 3.0$ ($n = 6$)). Thus, there was no evidence on this occasion that growth conditions were better in one area or the other, although due to the high rates of water exchange in the lagoon, the fish from the two sample sites may have been from the same biological "population."

In 1979, three much larger young-of-year (52–60 mm) were caught near the end of their 1st year of growth (November 14) in Stefansson Sound. We do not know if this relatively large size reflects accelerated growth during early winter, gear bias, or merely annual differences in young-of-year growth rates. Moskalenko (1964) observed that arctic cod growth continues through the winter months.

Older Arctic cod in Simpson Lagoon were 1–6 yr old but most were young fish, ages 1–3 (Table 2). Fish aged 4–6 comprised only 7% of the fish collected for age analysis and this is an overestimate of their proportion in the population as large fish were selectively chosen for age analysis. Inspection of the length frequencies shows that the sizes corresponding to age 1–3 fish (up to about 170 mm, Table 2) account for most of those caught (Fig. 3). An analysis of variance in fish length using three grouping variables (year (summers of 1977, 1978), age (2, 3), and sex (M, F)) showed that only age was a significant factor affecting the size of fish ($P < 0.001$). When sex was not used as a grouping factor (which meant that unsexed 1-yr-old fish were included), a two-way analysis of variance showed that age was again the most significant factor affecting the size of fish ($P \ll 0.001$). However, in this case the summer of capture was also a significant factor ($P < 0.003$), with the cod captured in 1978 tending to be larger than those captured in 1977.

The growth rate of cod in Simpson Lagoon is similar to that reported for other populations of this species caught in Prudhoe Bay (Bendock 1977) and nearshore waters of the Canadian Arctic (Bain and Sekerak 1978). However, the Simpson Lagoon fish were, on the average, 9–18 mm larger at each age compared with Arctic cod caught by otter trawl during the same period (August –September 1977) in deep offshore waters of the Beaufort Sea (Lowry and Frost 1981). A similar difference has been found in Pond Inlet in the Canadian High Arctic (M. Bradstreet, LGL Ltd., Toronto, Ont., personal communication) and in the southeastern Chukchi Sea/Norton Sound area (Wolotira et al. 1979). Perhaps warmer coastal waters provide more favorable growing conditions than offshore waters.

The length–weight relationship for summer-caught Arctic cod in Simpson Lagoon is

$$\log \text{weight (g)} = -5.196 + 3.031 \log \text{length (mm)}$$

$$n = 277, r = 0.98$$

SEX RATIO

Females generally outnumbered males but this was not always the case (differences tested by chi-square):

Season	*n*	% female	*P*
1977 summer	62	79	<0.001
1978 summer	69	80	<0.001
1978–79 winter	68	35	<0.025
1979–80 winter	33	75	<0.005
Totals	232	66%	

Age 1 cod were not included in these calculations because developing ovaries in small fish appeared easier to identify than testes. Older fish in the study population were primarily females, and they accounted for 74% of the 3- to 6-yr-olds. A predominance of females among older fish has also been reported in most other populations of Arctic cod (e.g. Moskalenko 1964; Bendock 1977; Bain and Sekerak 1978; Wolotira et al. 1979).

MATURITY

Assessment of age at sexual maturity was complicated by two factors: (1) most fish caught appeared to be immature, and (2) reproductive organs of mature fish were poorly developed in August and September when most Arctic cod were caught. Therefore, age at maturity was determined by considering only those fish that were known spawners or very probable spawners. "Known spawners" were ripe or spawned-out fish collected during the winter program; "very probable spawners" appeared to be approaching spawning condition in late summer and early winter samples. This assessment was based on analyses of egg sizes for females and the ratio of testes weight:body weight for males (Fig. 4).

Egg diameters were generally 0.2–0.5 mm in August and

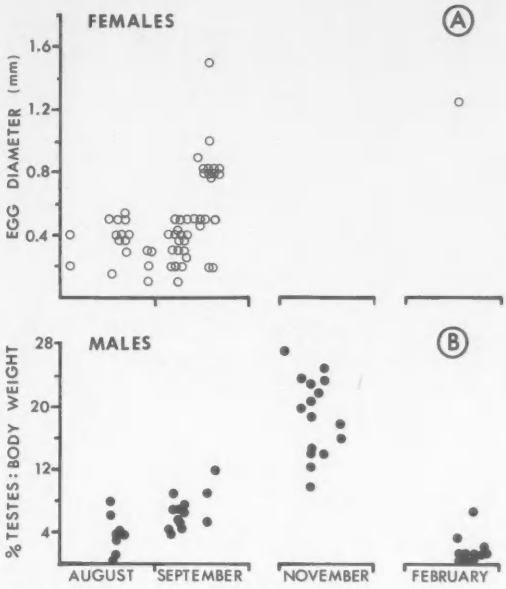

FIG. 4. Seasonal patterns of (A) egg sizes and (B) testes weight:body weight ratios of Arctic cod in summer (Simpson Lagoon) and winter (combined nearshore locations).

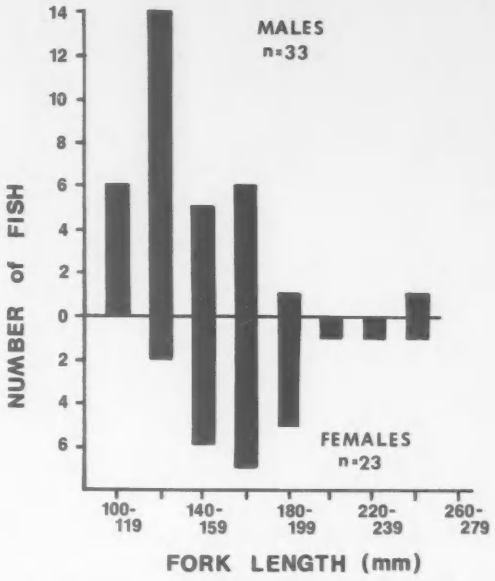

FIG. 5. Size composition of sexually mature Arctic cod.

early September. By mid-September, larger eggs (0.8–1.5 mm) were found in 12 female Arctic cod. These were considered to be maturing females because the eggs of the only ripe female caught nearly 5 mo later (February) measured 1.3 mm. Andriyashev (1954) reports that Arctic cod eggs reach 1.6–1.8 mm at spawning time in December and January.

For males, the ratio of testes weight:body weight showed a slight increase in August and September. In September, testes typically accounted for 4–8% of total body weight. These values increased to 10–27% for males judged to be mature in November. Lear (1979) recorded similar proportions (5.9–14.7%) for developing male Arctic cod in the northwestern Atlantic region.

The ages of these known or probable spawners were as follows:

Age	Number of spawners	
	Males	Females
1	2	0
2	13	3
3	14	11
4	2	4
5	1	2
6	1	1
Totals	33	21

Most mature males were ages 2 and 3 whereas most mature females were age 3. These ages at maturity are similar to those reported for this species in the northwest Atlantic Ocean (Lear 1979) and in the Soviet Union (Moskalenko 1964), although earlier than that listed (age 4) in Andriyashev's (1954) review of Soviet fishes. The proportion of Simpson Lagoon fish maturing at these young ages is not known. Some male fish classified as definite nonspawners in September and winter samples were ages 2 (n = 17) and 3 (n = 4), and some immature or nonspawning females were ages 2 (n = 49), 3 (n = 20), 4 (n = 1), and 5 (n = 1).

Sizes of mature males were generally smaller than those of mature females (Fig. 5), as one would expect from the sex differential in ages of maturity. Most mature males measured 107–160 mm long and, prior to spawning, their testes weight ranged from 1.4 to 12.9 g. However, testes weight for one old and large male (253 mm, age 6) was 56 g. Mature females tended to be between 140 and 180 mm in length with ovary weights of 1.2–6.0 g. These fish sizes are considerably smaller than the 200- to 230-mm (total length) range reported for spawners in Soviet waters (Andriyashev 1954).

SPAWNING PERIOD AND AREA

Spawning occurred sometime between late November and early February. Fish nearing spawning condition were caught in early winter (November 5–16, 1978, and November 11–14, 1979) and by February, spawning was essentially complete. At that time (February 17–23, 1979), 1 ripe and 5 spawned-out females and 14 spawned-out males were collected under the ice. On later winter sampling trips (April 30–May 12, 1979, and May 1–5, 1980), another spawned-out female and two males were taken. In Soviet waters, Arctic cod spawn in midwinter, usually from the end of December

TABLE 3. Food of Arctic cod in summer (Simpson Lagoon) and winter (Thetis Island to Narwhal Island, November 1978 and February 1979; 175 km offshore, May 1980). Percentages indicate proportion of total weight of each food item to the grand total weight of stomach contents in each collection.

	% composition (wet weight)				
	Summer nearshore			Winter nearshore	Winter offshore
Food item	1977	1978	1979	1978–79	1979–80[a]
Mysids					
Mysis litoralis	6	10	40	57	0
Mysis relicta	35	27	19	8	0
Remnants	47	2	[b]	28	0
Amphipods					
Onisimus glacialis	7	12	35	[b]	0
Gammarus setosus	[b]	0	3	0	0
Apherusa glacialis	0	0	1	0	9
Parathemisto spp.	2	0	0	0	4
Pontoporeia affinis	[b]	[b]	1	[b]	0
Miscellaneous spp.	[b]	0	[b]	[b]	0
Remnants	1	5	1	2	4
Copepods	2	44	1	[b]	22
Cumacea	0	0	[b]	[b]	1
Euphausiid	1	0	[b]	0	3
Fish	0	0	0	2	59
Miscellaneous spp.	[b]	0	0	2	0
No. stomachs examined	34	20	47	84	22
Mean size fish (mm)	160	109	92	125	92

[a]175 km offshore station.
[b]<0.5%.

to early February (Moskalenko 1964).

Fish judged to be potential spawners were distributed throughout the study area in November, but the 1 ripe and 19 recently spawned-out cod taken in February were all in Stefansson Sound. In general, few Arctic cod (spawning or otherwise) were collected in February at sites other than Stefansson Sound although this may be due to gear bias as previously mentioned. In addition, the offshore station, where the late-winter catch per unit effort was highest, was not sampled at this time, but two spawned-out cod were caught there in May 1980.

In late winter (May 3, 1980) we attempted to identify spawning areas of Arctic cod by determining the under-ice distribution of their pelagic eggs or larval stages. Replicate plankton tows were taken in a north–south transect with samples in Stefansson Sound and at 40-, 80-, 120-, and 175-km distances from shore. However, no cod eggs were collected and only a single 6-mm larval fish (presumably an Arctic cod) was found at the 40-km station. The relative importance of nearshore sites compared with regions farther offshore for spawning by Arctic cod remains unknown.

FOOD HABITS

In nearshore waters, epibenthic mysids were the major food item of Arctic cod (Table 3). During three summers and one winter of study when collections from nearshore waters were analyzed, *Mysis litoralis*, *M. relicta*, and mysid remnants accounted for 39–93% of the diet. Amphipods (*Onisimus glacialis*) and copepods were also eaten in appreciable quantities.

The diet of Arctic cod collected under the ice surface in offshore waters differed greatly from that described above. Here copepods, amphipods, and fish were the principal food items in the late-winter sample (May 1980). The significance of fish as a dietary item is probably much less than indicated because the high percentage (59% of diet) was due to the presence of relatively heavy fish remains in only 3 of the 22 stomachs examined. Copepods and amphipods, rather than mysids, also comprised most of the diet of 157 Arctic cod collected in offshore waters of the Beaufort and Chukchi seas during the open-water period in 1977 (Lowry and Frost 1981). In both of these situations (i.e. near-surface collections in winter and bottom collections in summer), pelagic amphipods (*Parathemisto* spp.) and an ice-associated amphipod (*Apherusa glacialis*) were important dietary items. Results from other studies conducted at different locations and times of year generally show that the principal foods of Arctic cod consist of varying proportions of mysids, amphipods, and copepods, although other zooplankters may be eaten as well (e.g. Andriyashev 1954; Tyler 1978; Bain and Sekerak 1978; Lilly 1979).

In our study, the dietary importance of the major groups of prey varied considerably among years; each was a major and minor dietary component at one time or another. This suggests that proportions of the various food items may be based on prey availability; however, limited evidence indicates that Arctic cod prefer to eat mysids rather than amphipods when

TABLE 4. Comparison of proportions of food items in winter diets of Arctic cod and in the environment using Ivlev's (1961) electivity index (E). Food items listed are those in which the percent composition in the diet and/or environment was 1% or greater.

	Simpson Lagoon, November 1978			Stefansson Sound, November 1978			Stefansson Sound, February 1979		
	% composition			% composition			% composition		
Food item	Diet	Environ.	E	Diet	Environ.	E	Diet	Environ.	E
Mysids	95	16	0.71	99	36	0.47	97	3	0.94
Amphipods	5	63	−0.87	1	18	−0.89	2	92	−0.96
Copepods				0.5	37	−0.97			
Cumaceans	0	8	−1.00	0	1	−1.00			
Isopods	0	5	−1.00						
Polychaetes	0	6	−1.00	0	8	−1.00	0	3	−1.00
No. samples	22	5		12	5		44	5	

both are available. The diet of Arctic cod was compared with the available food supply at sites where fish were caught during two winter collection periods at two nearshore locations, Simpson Lagoon and Stefansson Sound (Table 4). The high electivity indices for mysids (0.47−0.94) indicate a strong selection for this prey group. Although mysids are abundant in these nearshore waters in summer, they apparently move into deeper waters in winter thus accounting for their relatively low abundance at that time (Griffiths and Dillinger 1981). In contrast with the preference for mysids, the highly negative electivity indices for amphipods (−0.87 to −0.96) indicate that amphipods are either avoided by or inaccessible to Arctic cod. As some amphipod species burrow into the lagoon bottom (Griffiths and Dillinger 1981), their inaccessibility presumably contributes to the low electivity value. Similarly, cumaceans, polychaetes, and isopods are benthic invertebrates that may generally be inaccessible to Arctic cod.

Discussion

As Andriyashev (1954) remarked almost 30 yr ago, Arctic cod "occupies an extremely important place in the food chain of Arctic seas, being the main or only (if coastal regions are excluded) consumer of plankton . . . at the same time the Arctic cod serves as main food of many marine mammals (belukha, seal, Greenland seal, bearded seal, narwhal and others), birds (sea-gulls, Alcidae, skuas) and in some regions of fishes (cods, plaice, ruff)." It is somewhat surprising, then, that our understanding of Arctic cod biology is quite rudimentary. Available data from the Beaufort Sea are, however, in general agreement with the limited information available from other arctic regions.

Our study and others (Bendock 1977; OCSEAP 1978; Lowry and Frost 1981) indicate that the Arctic cod is perhaps the most widely distributed and abundant fish species in the Beaufort Sea. Some known temporal and spatial exceptions to this broad statement are that (1) Arctic cod are infrequent visitors to nearshore habitats during the first portion of the open-water season, and (2) they are outnumbered by other species near the mouths of some large rivers such as the Colville River and presumably the Mackenzie River with its diverse fish fauna.

Migration patterns of Arctic cod in the Beaufort Sea are essentially unknown except to say that in late summer, some migrate into coastal waters. This also occurs in the Canadian High Arctic (Bain and Sekerak 1978; Finley and Gibb 1982) and the Soviet Union (Andriyashev 1954; Nikolskii 1954; Moskalenko 1964). The large schools of fish that may form at this time have been described in the Soviet literature as prespawning migrations toward coastal spawning areas. The limited data available for Arctic cod in the Beaufort Sea tend to support this description. We are, however, uncertain about the overall importance of "nearshore" habitats versus "offshore" habitats in the life cycle of this fish. More specifically, does the nearshore environment of the Beaufort Sea provide important habitat for Arctic cod (analogous to the case, for example, of Pacific herring, *Clupea harengus*, which spawn along Pacific shorelines), or does this marine species accomplish its life cycle functions over large oceanic areas? The evidence is equivocal. First, although it is clear that many juveniles enter nearshore habitats such as Simpson Lagoon, possibly to benefit from the abundant food resources there (Craig and Haldorson 1981; Griffiths and Dillinger 1981), juveniles are also found at least 50−150 km offshore in summer (Lowry and Frost 1981) and at least 175 km offshore in winter (this study). Second, young-of-year Arctic cod are relatively abundant in coastal waters, but they too are present at least 40−110 km offshore (OCSEAP 1978; Hunter 1979) and a case has been made that those caught in Prudhoe Bay actually originated elsewhere and drifted toward shore with prevailing currents (Tarbox and Thorne 1979). Third, some adults likely spawned near shore because a few ripe and spawned-out fish were caught in Stefansson Sound in February; however, spawned-out fish were also collected 175 km offshore, albeit in late winter when considerable postspawning movements could have occurred.

Despite these uncertainties about Arctic cod, it is apparent from available data that the life history characteristics of this marine fish are quite different from those typified by many other arctic fish populations described in the literature. Freshwater and anadromous fishes in northern regions are frequently characterized by attributes which have become familiar: slow growth, late maturity, multiple-year spawning potential, and long life (e.g. Grainger 1953). The Arctic cod is, in contrast, a small, short-lived fish which matures at an early age and may, according to Nikolskii (1954), spawn only once in its lifetime. This trend holds even when the Arctic cod is compared with other cods (*Gadus* spp.) inhab-

TABLE 5. Growth and reproductive comparisons between Arctic cod and other Arctic and sub-Arctic cod species. Data sources: Nikolskii 1954; Andriyashev 1954; Leim and Scott 1966; Hart 1973; Salveson and Dunn 1976; Bain and Sekerak 1978; Ryan 1979; Wolotira et al. 1979; this study.

	Arctic cod (*B. saida*)	Atlantic cod (*Gadus morhua*)	Greenland cod (*G. ogac*)	Pacific cod (*G. macrocephalus*)
Maximum age	6–7	16	11	12
Maximum size (cm)	23–38	64–133	71–130	76–100
Size at age 5 (cm)	18–30	42–54	—	54–71
Age at maturity	2–3	6–10[a]	3–4	2–3(5–6)[a]
Fecundity ($\times 10^6$)	0.01[b]	5–9	1–9	1–3
Annual spawning	No?	Yes?	Yes?	Yes?

[a]In northern waters.
[b]A relatively low fecundity is at least partially due to the small size of mature fish.

iting more southerly latitudes.The Arctic cod has a smaller maximum size and shorter life span, and it matures at an earlier age than the Atlantic, Greenland, or Pacific cods (Table 5).

The kinds of life history characteristics exemplified by Arctic cod constitute a particular adaptation or "strategy" for life in their northern environment. One aspect of the relationship between such adaptations and the environment in which the population lives has been termed *r*- and *K*-selection (MacArthur and Wilson 1967; Gadgil and Solbrig 1972; Pianka 1974; Adams 1980). Life history characteristics of an *r*-selected species tend toward high productivity whereas those of a *K*-selected species tend toward efficient exploitation of a specific limiting resource with strong selection for individual fitness. Long-lived, slow-growing, and late-maturing northern fishes exemplify a *K*-type pattern or *K*-configuration (Johnson 1981, 1982), whereas the Arctic cod appears to exhibit an *r*-configuration. An *r*-selected species allocates a greater proportion of its resources to reproductive activities and this in turn implies that the population will be described by the following features (summarized by Adams 1980): (1) early maturity, (2) rapid growth rates, (3) production of larger numbers of offspring at a given parental size, (4) maximum production of offspring at early age, (5) small body size, (6) high rates of mortality, and (7) shorter life span. An *r*-configuration is optimal for a population living in an environment with a large component of unpredictable and nonselective or catastrophic mortality. In other words, it would not be advantageous for Arctic cod to invest its reproductive potential in large, long-lived individuals if mature fish are as vulnerable as juveniles to the principal sources of mortality.

Population sizes of an *r*-selected species are strongly influenced by physical factors in their environment. At first this seems improbable for Arctic cod because they live for much of the year in presumably stable conditions under protection of ice cover in the ocean. However, under certain circumstances, it appears that Arctic cod are susceptible to massive mortalities which have been observed at widespread locations in the Arctic. Typically in autumn or winter when the fish have moved close to shore, large numbers of dead Arctic cod have been found cast upon beaches in the USSR (Klumov 1937; Nikolskii 1954; Moskalenko 1964), the Canadian High Arctic (Bain and Sekerak 1978), and Alaska at Point Barrow and Cape Lisburne (Murdoch 1885; MacGinitie 1955; A. Springer, LGL Ltd., Fairbanks, AK, personal communication). Klumov reported that it is an annual event for polar bears and Arctic fox to feed upon Arctic cod thrown onshore by autumn storms, "in such huge numbers that the local population and winter scientific workers can collect enough for the whole winter, both for their own use and as food for their dogs." Bain and Sekerak (1978) reported thousands of Arctic cod stranded on the beach of Somerset Island and suggest that such occurrences are not uncommon in that area. They also mention that local Inuit believe Arctic cod strand themselves in an attempt to escape predation by marine mammals (see also Finley and Gibb 1982). At Cape Lisburne, Alaska, an estimated 19 000 Arctic cod were observed along a 3.2-km length of the beach (196 cod/33 m) after a large August 1978 storm (A. Springer personal communication), and both Murdoch (1885) and MacGinitie (1955) mention large numbers washing ashore during storms at Point Barrow, Alaska. These examples of large-scale mortality seem both nonselective and locally unpredictable, leaving one to reflect about the possible significance of such events on natural selection processes.

Population sizes of an *r*-selected species are less severely limited (than for a *K*-selected species) by density-dependent factors such as resources or predators. Theory suggests that, as an *r*-selected species, the fish are not regulated by the seabird and mammal populations which feed heavily upon them. If a regulatory effect does exist, it is probably exerted on the predators because population sizes of an *r*-selected species may be erratic, given the presumed controlling influence of variable, unpredictable, or catastrophic mortality factors.

Finally, Adams (1980) provides an interesting comparison of harvesting pressures on *r*- and *K*-selected species. Fisheries based on *r*-selected species will be more productive, as they can be fished at younger ages and at higher levels of fishing mortality. Adams concludes that, given a minimum population size, these fisheries should also have a quicker recovery time from overfishing. Thus, the implication here is that an *r*-selected species like Arctic cod might also recover more quickly from other kinds of perturbations (e.g. oil spill) than would the *K*-selected species like the char, ciscoes, and whitefish which also use coastal waters of the Beaufort Sea.

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Food, Feeding Habits, and Estimates of Daily Ration of the Shortfin Mako (*Isurus oxyrinchus*) in the Northwest Atlantic

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STILLWELL, C. E., AND N. E. KOHLER. 1982. Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 39: 407–414.

Analyses of the stomach contents of 399 male and female mako sharks (*Isurus oxyrinchus*) ranging from 67 to 328 cm are presented. Samples are from shark fishing tournaments held in New Jersey, New York, Rhode Island, and from longline catches taken between Cape Hatteras and the Grand Banks. Teleost remains occur in 67% of the stomachs with bluefish (*Pomatomus saltatrix*) constituting 77.5% of the diet by volume. Bluefish is the major inshore food item. Cephalopoda amount to 15% of the stomach contents by frequency of occurrence and are consumed primarily offshore. Consumption and diet are the same for both sexes. The average capacity of the stomach is 10% of the body weight. Estimates of daily ration average 2 kg (range from 1.4 to 2.7 kg). Makos may consume 4.3 to 14.5% of the available bluefish resource in the area between Cape Hatteras, NC, and Georges Bank.

Key words: shortfin mako, *Isurus oxyrinchus*; elasmobranchs, food habits, stomach content analyses, daily ration, *Pomatomus saltatrix*, biomass

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Nous présentons dans l'article qui suit les résultats d'analyses des contenus stomacaux de 399 makos (*Isurus oxyrinchus*) de longueur variant de 67 à 328 cm. Les échantillons proviennent de tournois de pêche des requins des États du New Jersey, New York et Rhode Island, et de prises à la palangre entre le cap Hatteras et le Grand banc. On trouve des restes de téléostéens dans 67% des estomacs, le tassergal (*Pomatomus saltatrix*) constituant 77,5% du régime en volume. Le tassergal est le principal aliment consommé à la côte. En fréquence d'occurrence, les céphalopodes constituent 15 % des contenus stomacaux et sont consommées surtout au large. Les quantités consommées et le régime sont les mêmes chez les deux sexes. La capacité moyenne de l'estomac est de 10 % du poids du corps. La ration quotidienne est estimée à 2 kg en moyenne (extrêmes de 1,4 et 2,7 kg). Les makos peuvent consommer de 4,3 à 14,5 % de la ressource disponible en tassergals dans la zone comprise entre le cap Hatteras, NC, et le banc Georges.

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THE shortfin mako (*Isurus oxyrinchus*) is found throughout the tropical and temperate zones of the Atlantic Ocean, in the eastern Atlantic from St. Helena to Scotland and southwest Norway, across the middle Atlantic, and from Brazil to Browns Bank southwest of Nova Scotia in the western Atlantic (Bigelow and Schroeder 1948; Smith 1957; Scattergood 1962; Tibbo et al. 1963; Bass et al. 1975). Included in this paper are data from 20 makos caught off the Tail of the Grand Banks during July 31 to September 2, 1979. These captures were made 800 miles (1 mile = 1.609 344 km) east of Browns Bank, and therefore extend the known range of the species in the northwest Atlantic.

Until recently, knowledge of the food and feeding habits of the mako in the northwest Atlantic was limited to anecdotal information from sport and commercial fishermen and published reports based on examinations of a few individuals. The earliest account was by Captain Nathaniel E. Atwood in 1866, who found a nearly intact swordfish in the stomach of a large mako (McCormick et al. 1963). Some years later Murphy (1919) reported a large bluefish (*Pomatomus saltatrix*) in a mako he examined. More recently Bigelow and Schroeder (1948), Backus (1960), and Lineaweaver and Backus (1969) provided lists of food items including scombrids, clupeids, other small fishes, and cephalopods. Large volumes of swordfish flesh or entire specimens weighing 54–66 kg have also been found in makos weighing over 318 kg (Bigelow and Schroeder 1948; Lineaweaver and Backus 1969).

The purpose of this study was to determine the basic foods

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of the shortfin mako in the northwest Atlantic and how its feeding habits relate to the biology and distribution of the species.

Methods and Materials

Data were collected at shark fishing tournaments and aboard research and commercial vessels using pelagic longlines. Tournament data were collected at annual contests held in New Jersey, New York, and Rhode Island during 1972–79. Longline data were from catches along the edge of the continental shelf between Cape Hatteras, North Carolina, and the Tail of the Grand Banks (Fig. 1).

To analyze the data for areal differences, tournament samples were considered inshore (<91 m depth) and longline catches were considered offshore (>91 m depth). Juveniles and adults of each sex were separated using minimum reproductive sizes of 170 cm FL (all lengths in this paper are fork lengths) for males and 270 cm FL for females (determined by H. L. Pratt, Northeast Fisheries Center, Narragansett Laboratory).

A total of 399 mako stomachs were examined including 183 females (from 74 to 328 cm FL) and 179 males (from 67 to 249 cm FL). Information from 37 additional fish for which no size or sex was reported was included in the total sample summaries only. Inshore and offshore samples were represented by 236 and 163 stomachs, respectively.

Stomachs were removed by cutting across the esophagus at the junction with the pharyngeal cavity and severing the middle stomach 5–8 cm posterior to the pyloric valve. Stomach contents were examined on site whenever possible. Samples collected aboard commercial vessels were stored on ice or frozen and delivered to the laboratory for examination. All prey items were identified to the lowest possible taxon, counted, and their volumes determined by water displacement. Food items not identifiable were fixed in 10% Formalin or frozen and returned to the laboratory for identification. Stomachs containing a few eye lenses or otoliths were considered empty. Baits were excluded from all volumetric determinations of stomach contents and were identified by smooth edged knife cuts, hook marks, and discoloration of skin and underlying fatty tissue.

Maximum stomach capacity was determined for a wide range of fish sizes. Empty stomachs were laid on a flat surface and filled with water under low pressure from a hose inserted 8–10 cm into the stomach. The anterior end of the stomach was held tightly around the hose to prevent water from escaping. When water was forced past the pyloric valve, the stomach was considered to be at its maximum capacity and the hose was removed. Water in the stomach was then measured to the nearest millilitre.

The major forage categories were evaluated as percentages by number, volume, and occurrence. Occurrence values were compared by area, size and sex, and season. Statistical analyses consisted of chi-square tests of significance ($P < 0.05$) and a paired t-test of differences between means.

Results and Discussion

Of the 399 stomachs examined, 273 (68.4%) contained food. Inshore, the percentage of stomachs with food (81.4%) was significantly higher than the percentage offshore (57.5%). Males and females within each area had approximately the same percentages of stomachs with food, 85.0 and 77.5% inshore and 58.5 and 56.8% offshore. The percentage of empty stomachs (31.6%) in the total sample is relatively low when compared with other studies on sharks (Strasburg 1958; Stevens 1973; Gubanov and Grigor'yev 1975; F. Williams, Rosenstiel School of Marine and Atmospheric Science, Univ. of Miami, Miami, FL 33419, personal communication).

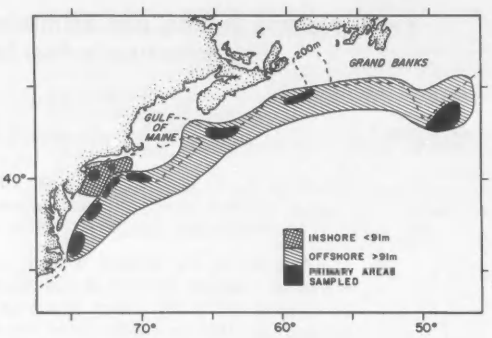

FIG. 1. Areas where 399 mako sharks were collected for food habits studies from 1972 to 1979. Sharks examined inshore were from sportfishing tournaments and those examined offshore were taken by longline on research and commercial vessels.

FOOD BY TAXONOMIC GROUPS

Teleosts — The forage category "all teleosts" was the major food group eaten by the mako shark by number (59%), volume (98%), and occurrence (67%) (Fig. 2). Of the 14 families of teleosts listed in Table 1, bluefish and scombrids were the most important prey and were represented in 51.3% of the stomachs. Bluefish occurred in 43.8% of the stomachs and amounted to 77.5% of the food by volume. Scombrids were found in 7.5% of the samples (Fig. 2). Sauries (*Scomberesox saurus*), clupeids (*Clupea* sp. and *Brevoortia tyrannus*), alepisaurids, and swordfish occurred in a few stomachs (Table 1).

The presence of small stones and the remains of demersal and benthic fish in some stomachs (Table 1) suggest that makos occasionally forage near or on the bottom. The stones may have been from the stomach of a food item or ingested while attacking prey. Stevens (1973) found stones in blue sharks that were feeding on bottom fauna.

Cephalopoda — Cephalopods were the second most important forage category by occurrence (Fig. 2). Originally, all beaks and body parts were classified as Cephalopoda. As the study progressed we attempted to identify them to family according to Clarke (1962) and Roper et al. (1969). Ommastrephidae, which includes *Illex illecebrosus*, occurred most often in our sample; this species occurs in the inshore and offshore waters of the study area in the spring, summer, and fall. *Loligo pealei*, another common squid occurring

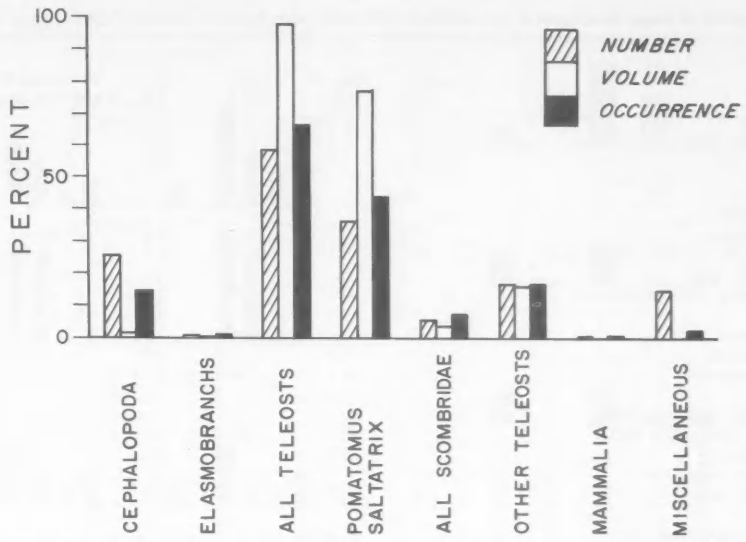

FIG. 2. The major forage categories occurring in 399 mako stomachs expressed as percentages by number, volume, and occurrence.

throughout the study area, was found in only one stomach. Three deep-water families, Gonatidae, Histioteuthidae, and Onychoteuthidae, were represented by beaks in 2.5% of the samples. Unidentified Cephalopoda occurred in 8.8% of the stomachs (Table 1).

Elasmobranchs — Our evidence suggests that elasmobranchs are unimportant in the mako's diet (Fig. 2). One stomach had a bite-sized chunk of blue shark, another contained remains of an eagle ray (*Rhinoptera* sp.), and two contained skate egg cases. A large mako examined by Applegate (1966) had eaten three carcharhinids, possibly blue sharks. Bass et al. (1975) also found remains of three species of sharks in 4 of 12 makos they examined. Thus, if conditions are right (e.g. a scarce preferred prey and many sharks, or sharks available in nets or on longlines) the mako may prey on other elasmobranchs.

Cetaceans — Cetacean remains were found in three stomachs. These consisted of skin-covered chunks of dense fatty tissue attached to dark red fibrous muscle. The skin in each case was smooth, grayish-black in color, and about 2 mm in thickness, similar to that of dolphin and porpoise. We have no evidence to indicate that the mako is a predator on living cetaceans. The only sharks presently recognized as predators of living cetaceans are *Centroscymus coelolepsis* and *Isistius brasiliensis* (Van Utrecht 1959; Jones 1971; Clarke and Merrett 1972).

Miscellaneous stomach items — The occurrence of anomalous food items or indigestable materials in the mako stomachs was relatively rare. Crustacea in one stomach were probably in the gut of a fish eaten a few days earlier because the flesh and bones were also present. Ctenophora in another stomach may have been engulfed accidentally during normal feeding. A small wad of sargassum weed (*Sargassum natans*) found in one stomach may have been ingested as the shark investigated debris at the surface. According to Strasburg (1958), pelagic sharks are opportunistic feeders and it is not unusual for them to consume items of little or no nutritive value.

ANALYSIS OF MAJOR FORAGE CATEGORIES BY AREA, SIZE AND SEX, AND SEASON

Variation by area — Inshore, makos showed a marked dependence on fish as food (86% by occurrence). A significant portion of the total volume of fish consumed were bluefish (85%) which occurred in 65% of the stomachs. Cephalopods constituted a small percentage of the diet (Fig. 3). This low percentage is difficult to explain considering the high inshore abundance estimates reported for *Illex illecebrosus* and *Loligo pealei* (Lange 1978; Lange and Sissenwine 1980). However, studies by Ivlev (1961), Ware (1972), and others indicate that predators tend to select the largest prey available. Thus, the makos seem to be selectively feeding on the larger, less abundant bluefish which would maximize their net rate of energy intake (Pyke 1979) assuming the amount of energy expended in capturing bluefish and/or squid is equivalent.

In offshore makos the utilization of fish as food (47% by occurrence) was reduced because of a decrease in the occurrence of bluefish in the diet. However, cephalopods became more important (22% by occurrence) (Fig. 3). Ommastrephidae and unidentified squid remains made up the majority of cephalopods. The remainder consisted of deep-water families (Gonatidae, Histioteuthidae, Onychoteuthidae). Evidence from Roper and Young (1975) indicates that the vertical distribution ranges of these and other deep-water squids coincide

TABLE 1. Checklist of forage items found in the stomachs of 399 mako sharks from the northwest Atlantic from 1972 to 1979.

	No. items	Num. % (*N*)	Vol. (mL)	Vol.% (*V*)	No. stomachs with food item	Frequency of occurrence (*F*)
Crustacea	42	6.3	3.0	0.0	1	0.2
Ctenophora	50	7.5	17.0	0.0	1	0.2
Molluscs						
Cephalopoda						
Decapoda (squid)						
Ommastrephidae	30	4.5	512.6	0.1	11	2.8
Illex illecebrosus (short-finned squid)	38	5.7	6127.0	1.2	4	1.0
Loliginidae						
Loligo pealei (long-finned squid)	1	0.1	25.0	0.0	1	0.2
Gonatidae	21	3.1	12.8	0.0	7	1.8
Histioteuthidae	3	0.4	0.2	0.0	2	0.5
Onychoteuthidae	1	0.1	0.0	0.0	1	0.2
Unidentified cephalopods	74	11.1	718.0	0.1	35	8.8
Elasmobranchs						
Carcharhinidae (requiem sharks)						
Prionace glauca (blue shark)	1	0.1	946.2	0.2	1	0.2
Rajidae (skates)	2	0.3	6.3	0.0	2	0.5
Myliobatidae (eagle rays)						
Rhinoptera sp.	2	0.3	400.0	0.1	1	0.2
Teleosts						
Anguillidae (freshwater eels)						
Anguilla rostrata (American eel)	1	0.1	775.0	0.2	1	0.2
Clupeidae (herrings)	6	0.9	95.0	0.0	2	0.5
Brevoortia tyrannus (Atlantic menhaden)	3	0.4	670.0	0.1	2	0.5
Alepisauridae (lancetfishes)						
Alepisaurus sp.	4	0.6	515.0	0.1	3	0.8
Gadidae (codfishes)	3	0.4	1182.8	0.2	1	0.2
Merluccius bilinearis (silver hake)	1	0.1	125.0	0.0	1	0.2
Zoarcidae (eelpouts)						
Macrozoarces americanus (ocean pout)	1	0.1	300.0	0.1	1	0.2
Scomberesocidae (sauries)						
Scomberesox saurus (Atlantic saury)	26	3.9	2080.0	0.4	5	1.2
Syngnathidae (pipefishes)						
Hippocampus erectus (lined seahorse)	1	0.1	5.0	0.0	1	0.2
Pomatomidae (bluefishes)						
Pomatomus saltatrix	241	36.1	379263.0	77.5	175	43.8
Sparidae (porgies)	1	0.1	30.0	0.0	1	0.2
Scombridae (mackerels and tuna)	23	3.5	11615.0	2.4	16	4.0
Euthynnus pelamis (skipjack)	1	0.1	1900.0	0.4	1	0.2
Scomber scombrus (Atlantic mackerel)	9	1.3	3150.0	0.6	9	2.2
Thunnus sp. (tuna)	5	0.7	2590.0	0.5	4	1.0
Xiphiidae (swordfishes)						
Xiphias gladius	2	0.3	60783.8	12.4	2	0.5
Stromateidae (butterfishes)						
Peprilus triacanthus	3	0.4	150.0	0.0	1	0.2
Scorpaenidae (scorpionfishes)	6	0.9	1970.0	0.4	3	0.8
Sebastes marinus (redfish)	4	0.6	1645.0	0.3	3	0.8
Triglidae (searobins)	1	0.1	250.0	0.1	1	0.2
Unidentified teleosts	50	7.5	9226.5	1.9	39	9.8
Mammalia	3	0.4	1595.0	0.3	3	0.8
Miscellaneous						
Sargassum weed	1	0.1	0.0	0.0	1	0.2
Stones	3	0.4	0.0	0.0	3	0.8
Animal remains	3	0.4	682.0	0.1	3	0.8
Totals	667		489366.2			

with the diurnal vertical movements of makos (F. G. Carey, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, personal communication). Thus, these deep-water squids along with other Cephalopoda contribute significantly to the food of the mako in offshore areas.

Variation by size and sex — With increasing predator size, more large prey were consumed in both areas (Fig. 3). This

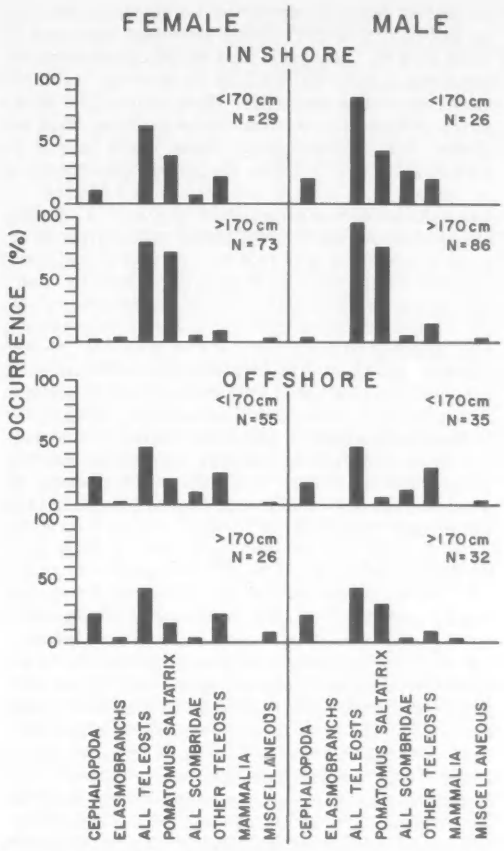

FIG. 3. Percent occurrence of the major forage categories found in mako sharks by area, size, and sex.

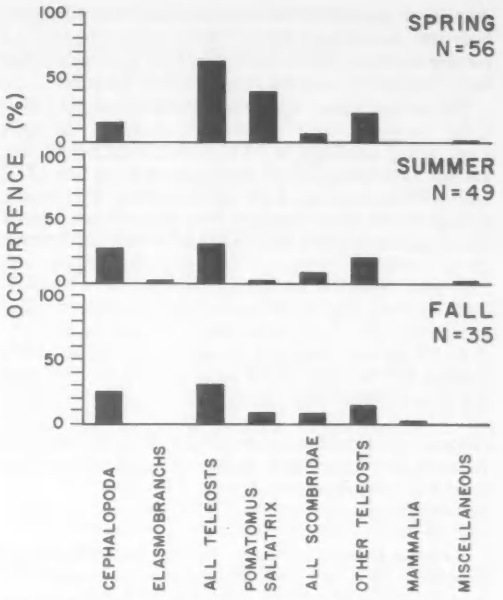

FIG. 4. Percent occurrence of the major forage categories found in the stomachs of 140 mako sharks captured offshore (>91 m) during the spring, summer, and fall.

trend, however, was not observed in the offshore females because of a lack of large individuals in the sample. Stomachs from two of the largest fish examined contained remains of swordfish. This was the largest prey item consumed by any makos in the study. A shift to very large prey such as swordfish occurs when makos attain sizes greater than 150 kg. At this weight, they are capable of attacking swordfish weighing 50–250 kg or more. Available data suggest that only female makos reach these larger sizes. Because so few of these big fish have been captured and examined we can only speculate that predation on swordfish and other large pelagics (tunas, marlins) occurs routinely.

A comparison of males and females by size and area showed no significant difference in their diet or in the amount of any of the major forage categories. Males and females were represented almost equally in both areas, but only 1 of the 183 females was mature (>270 cm). This inequality suggests that sexual segregation may occur when reproductive size is reached or that the fishing gear is selecting for the smaller individuals.

Variation with season — Data for seasonal changes in the diet were limited to sharks collected offshore from March through November. In the spring (March to May), teleosts were the primary food with bluefish the most important prey species (Fig. 4); cephalopods were relatively unimportant. By summer (June to August), most of the bluefish had migrated inshore (Wilk 1977) and rarely occurred in the diet; cephalopods increased in importance and approached "all teleosts" in their frequency of occurrence. In the fall (September to November), cephalopods and teleosts were of nearly equal importance as a food source; bluefish had begun to move offshore for the winter migration (Wilk 1977) and occurred with increasing regularity in the diet (Fig. 4).

Relationship of Body Size to Food Volume and Stomach Capacity

No significant differences were found in volumes of average stomach contents of males and females within and between each area (paired t-test, $P < 0.05$). Sexes from both areas were pooled and divided into three length classes: <170 cm, 170–220, and >220 cm. Analysis by length class showed that as length increased, average food volume increased because the larger makos eat larger food items. However, the average stomach content decreased per unit of body weight (mL/kg) as the fish weight increased. The same relationship was observed in studies of yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) by Reintjes and King (1953), King and Ikehara (1956), and in the squawfish by Thompson (1959). The pooled data also showed a

decrease in the number of empty stomachs with increasing body size. According to Ricker (1946), this is to be expected because small fish tend to digest their food more rapidly than larger individuals, resulting in more empty stomachs.

The average weight of food in the stomach of 183 makos (2 kg; converted from volume to weight on the basis 1 mL = 1 g) amounted to 2.6% of their body weight. The average food volume for all stomachs containing food (273) was 1793 mL and was 2.8% of the average body weight (63 kg) of 559 makos examined from the northwest Atlantic (Casey and Hoey 1980). In contrast, the average food content for all stomachs examined (399) including empties was 1226 mL (1.9% of the average body weight); this is comparable to data from Clark (1963) who reported that healthy sharks in captivity will eat 3–14% of their body weight per week (0.4–2% per day) depending on the size and species. Clark cautions that the consumption values may be low for sharks in a natural habitat where energy requirements for swimming and pursuit of prey is probably greater. Dragovich and Potthoff (1972) and Dragovich (1970) have shown that in the yellowfin and skipjack tuna (*Euthynnus pelamis*) the average volume of stomach contents was much less than 1.0% of the body weight.

Maximum stomach capacity — None of the stomachs were completely filled with food. To determine the fullness of a stomach, a ratio of the food content to the maximum liquid capacity of each stomach was calculated. Forty stomachs for which ratios were available averaged 19% (range 0.7–71%) of maximum capacity. Only one stomach from a 158-kg fish approached being full. The food consisted of 26 kg of swordfish that filled the stomach to 71% of its maximum. It is only on rare occasions that makos with full stomachs are examined as these individuals are probably least susceptible to capture. In addition, makos may digest large volumes of food at accelerated rates because of their elevated body temperatures (7–10°C above ambient) (Carey and Teal 1969). Magnuson (1969) described the work of several authors who found that as body temperature increased the time for a stomach to empty decreased. In the present study the average capacity of the mako stomach was 10% of the body weight. The maximum capacity measured was 23.3%. Magnuson (1969) reported the maximum stomach capacity for confined skipjack tuna to be about 7% of the fishes' weight.

Estimates of Daily Ration and Bluefish Biomass Consumption

Daily ration — Estimates of daily ration for the mako were derived from an energetics approach and by use of the average weight of the stomach contents. In studies on four squaloid species, Brett and Blackburn (1978) reported that the average routine metabolic rate was 106 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ (at 13°C). Adjusting the latter rate upward to a temperature of 18.8°C (mean environmental temperature of makos north of Cape Hatteras, NC; J. G. Casey, Northeast Fisheries Center, Narragansett Laboratory, personal communication) and using a Q_{10} of 2, the metabolic activity increases 1.49 times, resulting in a routine metabolic rate of 157.9 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$. Compensating for a body temperature 7–10°C above ambient (midpoint 8.5°C) and assuming a Q_{10} of 2, we derived an increase in metabolic activity of 1.8 times, or 284.2 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ at 27.3°C. Using an energy equivalent of 13.59 $J \cdot mg\ O_2^{-1}$ (quoted in Brett and Blackburn 1978), we found that 3.86 $kJ \cdot kg^{-1} \cdot h^{-1}$ or 92.46 $kJ \cdot kg^{-1} \cdot d^{-1}$ was needed for routine metabolism. If we assume 27% of the energy of ingested food is lost through excretion (Brett and Groves 1979) the total energy intake would have to be 1263.56 $kJ \cdot kg^{-1} \cdot d^{-1}$. Taking the average caloric value of the primary foods eaten by the mako to be 4.51 $kJ \cdot g^{-1}$, a 1-kg mako would have to consume 27.9 $g \cdot kg^{-1} \cdot d^{-1}$ for routine metabolism. Assuming the average mako weighs 63 kg, it would require 1.8 kg of food per day. Over a year, this is equivalent to 10.4 times the average body weight for routine metabolism. To compensate for energy expended during periods of active metabolism (prey search, attack, and migration), food consumption could increase a minimum of 25–50% (Brett and Blackburn 1978; Brett and Groves 1979), resulting in a daily ration of 2.2–2.7 kg and an annual consumption as high as 12.7–15.6 times the average body weight.

The second estimate of daily ration was based on the average weight of the stomach contents. We assumed that temperature and rate of food consumption were constant. An evacuation rate (R) was calculated from an equation in Elliot and Persson (1978):

$$(1) \quad S_t = S_0 e^{-Rt}$$

where S_0 and S_t are the amount of food in the stomach at the beginning and end of t hours, and R is the exponential rate of gastric evacuation. Assigned values for t of 36 and 48 h were made with the assumption that all but 10% (0.1226 kg) of the initial food would be evacuated in these time periods. The hourly estimates were based on field observations of mackerel baits from blue shark (*Prionace glauca*) stomachs after 10 and 26 h and from the digested condition of bluefish removed from mako stomachs examined on 2 consecutive days at fishing tournaments over a period of 5 yr. Assuming a t of 36 h and an S_0 value of 1.226 kg, we derived an R value of 0.0639 $kg \cdot h^{-1}$. The daily ration ($\Sigma C(t)$) was then calculated by:

$$(2) \quad \Sigma C(t) = 24\bar{S}R$$

(Elliot and Persson 1978) where $\bar{S}$ is the mean weight of stomach contents (1.226 kg) over 24 h. The daily ration was 1.9 kg. When a t value of 48 h was used, an R value of 0.0479 $kg \cdot h^{-1}$ was derived which resulted in a daily ration of 1.4 kg. R values for both estimates of t were within the range of experimentally derived values in studies summarized by Durbin and Durbin (1980) where fish were fed fish flesh. Annual consumption based on the average weight of stomach contents ranged from 8.0 to 11.0 times the average body weight; this is in close agreement with the value determined by the bioenergetics method before an allowance was made for periods of active metabolism. An overall daily ration of 2 kg resulted from averaging the estimates derived by the two methods.

Bluefish consumption — Bluefish constitute 77.5% (by volume) of the mako diet. To determine the impact of makos on the bluefish resource between Cape Hatteras, North

TABLE 2. Estimates of the feeding impact that the mako population between Cape Hatteras and Georges Bank has on the bluefish resource.

Mako			Bluefish			
Fishing mortality	Biomass (t)	% of body[a] weight	No. days[b]	% of diet[c]	Biomass consumed	% Total biomass
10.0%	2952	3.1	240	77.5	17021	14.5
20.0%	1476	3.1	240	77.5	8510	7.3
33.3%	886	3.1	240	77.5	5108	4.3

[a]Represents an average daily ration of 2 kg expressed as a percentage of the average body weight of 63 kg.

[b]The estimated number of feeding days that bluefish are likely to occur in the makos diet between Cape Hatteras and Georges Bank.

[c]The percentage by volume of bluefish that was observed in the makos diet.

Carolina, and Georges Bank, we calculated biomass estimates for each species. For the bluefish, a biomass of 117 003 t was derived using data from E. D. Anderson (Northeast Fisheries Center, Woods Hole Laboratory, personal communication). The mako biomass was estimated on the basis of an MSY of 295 t deduced from data in Anderson (1980) and from a mako to all shark catch ratio of 5.2% (J. G. Casey and J. J. Hoey, Northeast Fisheries Center, Narragansett Laboratory, personal communication). Assuming that the 295 t represented fishing mortalities of 10, 20, or 33.3% (Tiews 1978) of the mako population, we derived total biomass estimates of 2952, 1476, and 886 t. Our data suggest that makos may have an estimated residence time in the area of 240 d. If we assume this coincides with the number of feeding days, then from 5108 to 17 021 t (4.3–14.5%) of the available bluefish biomass could be consumed depending on which biomass estimate is used for the makos (Table 2). It appears from these calculations that although bluefish are a major food for the mako, the impact on the bluefish population over 240 feeding days is not significant.

Daily ration and biomass consumption of natural fish populations are difficult to estimate and are at best only approximations. This is particularly true for large predatory species. Several factors including ambient temperature, predator, meal, and food size, composition of diet, feeding frequency, and number of feeding days all play an important role. The mako shark as a large active predator adds two unique variables to the list. One is an elevated body temperature and the second is a controllable heat exchanger (Burne 1923; Carey et al. 1978) that can warm or cool the blood flowing to the viscera. Their streamlining suggests speed and because of this and their warm-bodied temperatures, Brett and Blackburn (1978) suggest the metabolic capacity of the mako could approach that of highly evolved teleosts.

Acknowledgments

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Limited Entry Policy and the Bristol Bay, Alaska Salmon Fishermen

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The impact of limited entry was examined upon the diverse groups engaged in the Bristol Bay, Alaska salmon fishery. Whereas limited entry was intended to enhance the state's rural fishing economies, the system has in fact significantly diminished access of the local population to the fishery, the region's primary economic activity. A significant proportion of local fishermen were intially denied entry permits due to entry criteria in which the implicit definition of a legitimate fisherman was based largely upon a nonrural model, development of an application poorly designed for use by the rural Alaskan population, and administration of the program by a bureaucracy that appears insensitive to the needs of the rural communities. The salability of the permits, combined with the poorer fishing earnings of local fishermen and the generally impoverished local economy, led to a further drain of permits from local areas. Unless the system is substantially altered, local fishing communities can be expected to suffer significant further impoverishment because the fishery is now effectively closed to their burgeoning youthful population. However, the present system substantially benefits urban Alaskan fishermen (as well as non-Alaskan fishermen), who are more effective politically than their rural counterparts, so no substantial change in the present system can be expected. Limited entry programs clearly must be based upon a better understanding of the socioeconomic and cultural characteristics of targeted fishing communities if such highly inappropriate consequences are to be avoided.

Key words: limited entry, Bristol Bay, salmon fishery, socioeconomic, *Oncorhynchus nerka*, fishery management

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Nous avons analysé l'impact de l'accès limité sur les divers groupes pratiquant la pêche du saumon dans la baie de Bristol (Alaska). Bien que l'accès limité ait visé à rehausser l'économie de la pêche dans les régions rurales de l'État, le résultat en fut tout autre. En fait, l'accès a été nettement réduit pour la population locale, dont la principale activité économique était la pêche. Une proportion significative des pêcheurs locaux se sont vu refuser des permis par suite de critères définis d'après un modèle non rural; d'un formulaire d'application mal conçu pour utilisation par les populations rurales de l'Alaska; et enfin, de l'administration du programme par une bureaucracie apparemment insensible aux besoins des communautés rurales. La fait que les permis pouvaient être vendus, couplé aux faibles revenus que les pêcheurs locaux retiraient de la pêche et à une économie locale affaiblie, a accéléré cette saignée des permis de pêche des régions locales. À moins que l'on ne modifie le système, on peut s'attendre que les communautés de pêche locales s'appauvriront encore davantage car la pêche est présentement hors de la portée d'une jeunesse montante. Par contre, le présent système profite de façon substantielle aux pêcheurs urbains de l'Alaska (ainsi qu'aux non-résidents), jouissant d'une influence politique supérieure à celle de leurs homologues ruraux. On ne peut donc s'attendre à de grands changements au système actuel. Sûrement, des programmes d'accès limité doivent être fondés sur une meilleure compréhension des caractéristiques socio-économiques et culturelles des communautés de pêche visées, si l'on veut éviter des conséquences aussi désastreuses.

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FISHERIES in western countries have traditionally been open to all who obtained the necessary license and gear. However, resource economists have argued that open access has led to the characteristic economic inefficiency of most fish harvests and low economic status of most fishermen (Gordon 1954; Crutchfield and Pontecorvo 1969). As this argument has taken hold, limited entry programs have been introduced in a number of fisheries. However, despite increasing use of limited entry in fisheries management and growing controversy in regard to its implications (e.g. Crutchfield 1979; Cicin-Sain 1979), the socioeconomic consequences of limited entry have in fact been little studied.

The socioeconomic impact of limited entry upon a fishery will depend upon characteristics of both the fishing community and the particular entry program. The critical elements of a limited entry system are typically the allocation of the entry permits, their ownership, and transferability. What criteria are to be used to ensure the permits are distributed equitably? Are entry permits to remain the property of the state or should they devolve to the recipients? How are succeeding generations to enter the fishery? At this time, little is known of how different groups of fishermen are affected by the particular way these issues are resolved. Indeed it is not clear how fishing communities weigh the fundamental trade-offs among promise of economic gain and loss of flexibility for the entrants and loss of opportunity for those denied access in the changeover from an open access system (Crutchfield 1979; Cicin-Sain 1979).

The Bristol Bay, Alaska salmon fishery appears particularly well-suited to a study of the impact of limited entry. The fishery is conducted by several major groups of North American fishermen: full- and part-time fishermen; fishermen with and without alternative incomes; fishermen with traditional roots in fishing of both European and Native-American descent, as well as more recent entrants. In Bristol Bay, the impact of limited entry upon these diverse groups can be viewed within a single context.

Bristol Bay has also been the focus of considerable debate on limited entry. Crutchfield and Pontecorvo (1969) used the fishery as a classic example of a fishery in need of limited entry on grounds of economic efficiency. Although the fishery is highly valuable (it is based on the world's largest run of sockeye salmon (*Oncorhynchus nerka*)) it has historically been managed largely through gear and vessel restrictions, designed to limit the effectiveness of each fisherman, thereby increasing employment in the fishery.

However, when limited entry was instituted in Alaskan salmon fisheries in 1974, it was not on the basis of theoretical economic considerations, but in the face of the severe economic crisis in Bristol Bay and other parts of rural Alaska that had followed several years of exceptionally poor salmon returns (Adasiak 1977; Rogers 1979). An explicit effort was made to incorporate both social and economic criteria in determining eligibility for a permit under the Alaskan limited entry system: residence (rural vs. urban) and dependence upon fishing income, as well as experience in the fishery, served as criteria in awarding permits (compare Adasiak (1979) with Campbell (1973) and Fraser (1979) on the Canadian limited entry system for salmon). Although the system has been highly controversial (a statewide referendum unsuccessfully attempted to overturn it in 1976 and ~200 lawsuits have challenged it in the courts) it has been considered generally successful by its managers (Adasiak 1979).

Bristol Bay thus seemed particularly appropriate for the study of the socioeconomic impact of a limited entry system due to the diversity of groups within the fishery, the apparent need for limited entry regulation, and the manner in which the system was initially framed.

Methods

The study was conducted in June–August, 1979, through a combination of structured and unstructured interviews administered by a survey team consisting of the author, who had fished in Bristol Bay in the 1970 and 1971 seasons, a graduate student of anthropology (M. K. Gilliland, University of California, San Diego), and six volunteers recruited through the Center for Field Research (Earthwatch). Standard questionnaires were administered to captains of fishing vessels, experienced crewmen, and local villagers, and less formal interviews were conducted with cannery superintendents, fishermen's union officials, local community leaders, and numerous fishermen and residents.

Systematic sampling of the fishery population was facilitated by the physical structure of the fishery. Fish processing plants are located primarily in the villages of Naknek and South Naknek, situated on either side of the Naknek River (Fig. 1). The vast majority of Bristol Bay fishermen are not permanent residents of these villages. Because there is no surplus housing in the villages, nonresident fishermen depend upon the canneries for their housing as well as their market. Thus the fishermen could be readily surveyed in their quarters or on their vessels during nonfishing periods.

The captains who were interviewed were selected systematically from the processors' complete lists of captains under contract, which were obtained from five of the eight major canneries. Approximately 20 captains were selected from each cannery. After selecting the first name at random, between every third and every seventh name was selected for the survey, depending upon the number of fishermen on the list. Crewmen associated with the vessels were interviewed if they had fished for 5 yr or more in Bristol Bay.

To survey Bristol Bay residents, interviews were conducted in households in four villages within the Naknek–Kuichak watershed area: Naknek, South Naknek, Nondalton, and Kokhanok (see Fig. 1). These villages represent a gradient in their degree of contact with the outside world. Naknek is the center of the salmon processing industry in Bristol Bay and contains various commercial establishments to service the fishing industry as well as government offices. South Naknek is situated on the other side of the Naknek River. Transport between the villages is by air or boat at high tide. South Naknek is a smaller village, and although it contains several fish processing plants, it has none of the support services; it also has no direct ground link to the airport at King Salmon, which connects the area to the outside world. Nondalton and Kokhanok are situated upriver on the major sockeye salmon spawning grounds (Fig. 1). They are far removed from any large-scale commercial activity, although their residents depend heavily upon the fishery for cash income and upon the upriver salmon for subsistence. Residents of these villages represent the major Native groups in the area. Nondalton is an

FIG. 1. Bristol Bay and surrounding area showing the location of villages and places mentioned in the text. The Naknek–Kuichak fishery is conducted in the area delimited at the head of Bristol Bay.

Athabascan Indian village, and Kokhanok is predominantly Eskimo. Kokhanok was also selected because its residents had been aquainted with the author in 1970–71; this was felt to be a considerable advantage due to the short time available for the study and the general mistrust of strangers in more remote villages.

The surveys of Naknek and South Naknek were based upon the Borough Tax Assessor's maps and property lists and were conducted during the fishing season. The surveys of Nondalton and Kokhanok were based on a mapping of all residences in the villages, prepared in conjunction with local residents. I surveyed the upriver villages at the end of the fishing season. Village samples were selected systematically after enumerating all residences in the village. Depending upon size, every second to every fourth household was selected for the survey. The head of each household was the only person actually interviewed, but questions concerning all household members were asked.

All questionnaires covered the demographic characteristics of the respondent and his immediate family: their involvement in fisheries, particularly in Bristol Bay; the impact of limited entry policy on the household's fishing income and fishing strategy; and both closed and open-ended questions concerning the respondent's views on limited entry and its effect on various groups of participants in the fishery. The questionnaire administered to fishing captains also contained questions concerning vessel and gear characteristics, and these questions were also asked of those heads of village households who held limited entry permits. The interviews were ~1 h in length and were conducted orally; responses to the questions were recorded on survey forms by the interviewer. (Copies of the questionnaire forms may be obtained from the author).

The structured surveys were coded and analyzed first by the overall frequency of responses and broken down by captains, crewmembers, and local residents. The data from the fishermen were broken down by ethnic grouping and by place of residence (i.e. Bristol Bay area, greater Alaska, or outside Alaska). Data obtained from the villages were separated by village; the total village census was also broken down by age, sex, and ethnic group.

Results

The total resident population of Bristol Bay area is ~4600 (Kresge et al. 1974). 1717 permanent permits have been issued for drift gillnetting. A total of 113 questionnaires were completed. Of the respondents, 42 were captains, 14 were crewmembers, and 57 were heads of households in the villages of Naknek, South Naknek, Nondalton, and Kokhanok. The average household contained 4.1 inhabitants; a total of 235 residents were included in the village survey. Of the 66 households selected to be surveyed, 21 were located in Naknek, 14 in South Naknek, 17 in Nondalton, and 14 in Kokhanok.

Interviews were successfully obtained from 86% (57 of 66) of the village households selected for the survey; 97% of fishing captains contacted were successfully interviewed. However, only 47% of fishing captains selected for the survey were successfully contacted due to fishermen on company lists who either did not show up that year, left early, or chose to fish other Bristol Bay runs (e.g. Egegik or Dillingham; see Fig. 1); also, one cannery list could only be obtained near the end of the season, so few interviews could be completed there (24% of fishermen selected). The canneries were visited repeatedly, and due to a lengthy price dispute during which the fishermen remained ashore, 89% of captains selected from the four major canneries studied and known to be on the fishing ground were contacted. Although 45% of the crewmen aboard vessels that were surveyed had fished 5 yr or longer, only 14 were interviewed. Due to the low numbers of crewmen interviewed, this aspect of the study will not be discussed in detail.

DEMOGRAPHY

The ethnic background and residence of Bristol Bay fishermen are closely linked. The Bristol Bay fishery is dominated by non-Alaskans, primarily Italian-Americans living along the coast of California, as well as Scandinavian-Americans living primarily in the Pacific Northwest (Tables 1–3). These ethnic groups (hereafter referred to as the European ethnic fishermen) were among the first to exploit the Bristol Bay runs commercially (Rogers 1972). Local residents (80% of whom are Native-Americans) comprise 36% of the fishing fleet, and the remainder of the fleet is made up of non-Bristol Bay Alaskan residents, who have no dominant ethnic identity (Langdon 1980). Non-Alaskan fishermen tended to be over-represented in the survey of fishing captains, and Bristol Bay residents were under-represented (Tables 1 and 2) due to the major canners' historic and continued reliance upon non-Alaskan fishermen. Local residents tend to fish for smaller processors and buyers (less reliable markets) that could not be adequately sampled. The survey of local residents compensates for this deficit in the number of local fishing captains in the cannery-based survey.

TABLE 1. Residence of recipients of Bristol Bay drift gillnet permits (August 29, 1979) (from Langdon 1980).

	Residence					
	Bristol Bay		Greater Alaska		Non-Alaska	
	No.	%	No.	%	No.	%
Original permits issued	662	38.6	327	19.0	728	42.4
Changes due to transfers Jan. 1, 1975–Aug. 20, 1979	−43	−6.5	+14	+4.3	+29	+4.0
Residence following transfers	619	36.1	341	19.9	757	44.1

TABLE 2. Ethnic origin of the questionnaire respondents. "Native" refers to Eskimos, Aleuts, and Indians and "European" refers to persons with Italian, Scandinavian, or Croatian ancestry. Percentages are of column totals. (Missing observations: 3.)

	Questionnaire type							
	Captain		Crew		Village survey		Row totals	
Ethnic origin	No.	%	No.	%	No.	%	No.	%
Native	8	17.4	2	22.2	44	80.0	54	49.1
European	23	50.0	5	55.6	1	1.8	29	26.4
Other	15	32.6	2	17.2	10	18.2	27	24.5
Column totals	46	41.8	9	8.2	55	50.0	110	

TABLE 3. Residence of the questionnaire respondents by ethnicity. Percentages are of column totals. (Missing observations: 4.)

	Ethnicity							
	Native		European		Other		Totals	
Residence	No.	%	No.	%	No.	%	No.	%
Bristol Bay	49	90.7	2	6.9	9	34.6	60	55.0
Greater Alaska	2	3.7	3	10.3	7	26.9	12	11.0
California/ Oregon/ Washington	2	3.7	24	82.8	8	30.8	34	31.2
Other	1	1.9	0	0.0	2	7.7	3	2.8
Totals	54	49.5	29	26.6	26	23.9	109	

The Bristol Bay fleet is composed primarily of older fishermen (Table 4); 72% of captains surveyed were more than 35 yr of age, and more than half of these were over 50. Langdon (1980) found the mean age of Bristol Bay drift gillnet captains to be 42.0 yr.

On the other hand, the age distribution of the local communities is skewed considerably toward younger ages. In 1970, the median age of the Bristol Bay Native population was 17.6 yr, and 39% of the heads of village households surveyed were under 36 yr. The birth rate of the Bristol Bay Native population in 1970 (24.8 per 1000 population) was 14% higher than that of the non-Native Alaskan population and 36% higher than the national average (Langdon 1979).

CHARACTERISTICS OF FISHERY GROUPS

The major demographic groups that fish Bristol Bay can be further characterized in terms of their self-perception as fishermen, their involvement in fishing activities, their dependence upon Bristol Bay and other fisheries for their livelihood, the types of vessels and gear they use in Bristol Bay, their earnings from the fishery, and their activities when not

TABLE 4. Age distribution of captains and villagers. Percentages are of column totals.

	Questionnaire respondents			
	Captains		Villagers	
Age	No.	%	No.	%
≤24	7	15.2	136	61.8
25–35	6	13.0	26	11.8
36–50	14	30.4	29	13.2
51–65	15	32.6	15	6.8
>65	4	8.7	14	6.4
Totals	46	17.3	220	82.7

fishing in Bristol Bay (i.e. the remaining 10–11 mo of the year).

Both Bristol Bay resident and non-Alaskan fishing captains (but not captains from the greater Alaska area) tended to perceive themselves as "fishermen" (Table 5). Social and cultural rather than economic factors seemed the basis for this difference in self-definition by the major fishery groups. Only the non-Alaskans were significantly involved in other fisheries, and less than half (43%) of fishing captains, even in this group, were active in other fisheries. There was no significant difference in the degree to which the different groups depended upon fishing for their livelihood; 44–54% of fishermen in all groups depended upon fishing for more than two-thirds of their income. However, local residents were more dependent upon the Bristol Bay fishery per se (Table 6) (comparison of local vs. nonlocal fishermen obtaining less then two-thirds or more than two-thirds of income from Bristol Bay fishery: $\chi^2 = 4.09$, df = 1, $P < 0.025$). However, both Bristol Bay residents and non-Alaskan fishermen tended to have been brought up in families in which the father fished and to have started fishing while still boys (18 yr of age or younger), whereas those fishing from the greater Alaska area were generally brought up in nonfishing families and first fished as adults (Tables 7 and 8 ($P < 0.01$ and $P < 0.025$, respectively, Fisher exact test)).

Local residents lacked other opportunities to earn money and tended to be more dependent upon the Bristol Bay fishery. The village survey indicated more than half (59%) of all watershed resident men between the ages of 18 and 65 were currently engaged in the Bristol Bay fishery. The modal response of local residents when asked what they did during most of the remainder of the year when not fishing in Bristol Bay was either nothing or some form of rural activity (e.g. subsistence activity, trapping, or guiding) (46%), whereas nonlocal fishermen tended to be engaged in some form of blue-collar work (40%). The seasonal nature of employment in the region can be seen in Fig. 2.

Local residents were not only more dependent upon the Bristol Bay fishery for their income (Table 6), but they earned significantly less from it. In the period 1975–77, Langdon (1979) found the average earnings of Bristol Bay residents were 15% less than the fleet average. This results largely from the considerable disparity between the vessels and gear fished by local and nonlocal fishermen. Whereas virtually all nonlocal fishermen surveyed (98%) fished from the maximum regulation-size 32-foot (9.8-m) gillnetter, 43% of local captains either had no vessel or fished from open skiffs. Skiffs are less seaworthy and, due to prevalent windy and stormy conditions, they are unable to fish as many days as regulation-size gillnetters. The fish-holding capacity of local fishing vessels was also typically less (Table 9), which limits the fishermen's earnings, particularly during a good season and during the

TABLE 5. Response to question, "Do you consider yourself a fisherman?" by place of residence. Percentages are of column totals. (Missing observations: 3.)

	Residence							
	Bristol Bay		Greater Alaska		Non-Alaska		Totals	
Response	No.	%	No.	%	No.	%	No.	%
Yes	13	81.3	4	36.4	25	67.6	42	65.6
No	3	18.8	7	63.6	12	32.4	22	34.4
Totals	16	25.0	11	17.2	37	57.8	64	

TABLE 6. Fraction of captains' annual income derived from the Bristol Bay fishery alone, by place of residence. Percentages are of column totals. (Missing observations: 16.)

	Residence							
	Bristol Bay		Greater Alaska		Non-Alaska		Totals	
Fraction	No.	%	No.	%	No.	%	No.	%
<1/3	2	15.4	2	25.0	12	40.0	16	31.4
1/3–2/3	4	30.8	3	37.5	12	40.0	19	37.3
>2/3	7	53.8	3	37.5	6	20.0	16	31.4
Totals	13	25.5	8	15.7	30	58.3	51	

TABLE 7. Incidence among captains of fathers who had fished, by residence. Percentages are of column totals. (Missing observations: 6.)

	Residence							
	Bristol Bay		Greater Alaska		Non-Alaska		Totals	
Father had fished	No.	%	No.	%	No.	%	No.	%
Yes	14	82.4	1	10.0	28	82.4	43	70.5
No	3	17.6	9	90.0	6	17.6	18	29.5
Totals	17	27.9	10	16.4	34	55.7	61	

TABLE 8. Age at which Bristol Bay captains and crew first fished, by residence. Percentages are of column totals. (Missing observations: 7.)

	Residence							
	Bristol Bay		Greater Alaska		Non-Alaska		Totals	
Age	No.	%	No.	%	No.	%	No.	%
≤18	28	73.7	4	40.0	32	84.2	64	74.4
19–29	6	15.8	2	20.0	4	10.5	12	14.0
≥30	4	10.5	4	40.0	2	5.3	10	11.6
Totals	38	44.2	10	11.6	38	44.2	86	

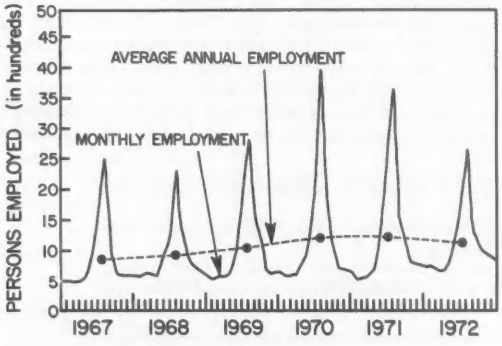

FIG. 2. Employment patterns in Bristol Bay area, 1967–72, showing the seasonal nature of monthly employment and average annual employment. (Source: Kresge et al. 1974.)

peak of the run during a poorer year. As expected, the estimated value of local fishing vessels was also substantially less (Table 10). Nonlocal fishing captains typically owned more fishing gear as well, 76% owning more than the three shackles (91.4 m) of gill net permitted to be fished at one time, thus maintaining a reserve, whereas only 36% of local fishermen owned more than three shackles of gear.

LIMITED ENTRY AND BRISTOL BAY FISHERMEN

Bristol Bay residents and nonlocal fishermen were sharply divided in their views of Alaskan limited entry policy (Table 11). A majority of both local and nonlocal fishermen felt the present system should be modified, but the two groups proposed fundamentally different modifications. Nonlocal fishermen were predominantly in favor of tightening the existing system (i.e. more enforcement, halting the issuance of additional permits), whereas Bristol Bay residents considered the present system too restrictive and generally believed more permits should be issued to the local population (Table 12). A substantial proportion of nonlocal fishermen (41%) favored retaining the limited entry system in its present form, a view with virtually no support among local residents; a significant

TABLE 9. Capacity of captains' fishing vessels (in number of sockeye the vessel can hold), by the place of residence. Percentages are of column totals. (Missing observations: 13.)

	Residence							
	Bristol Bay		Greater Alaska		Non-Alaska		Totals	
Boat capacity	No.	%	No.	%	No.	%	No.	%
<3000	8	61.5	2	20.0	8	25.8	18	33.3
>3000	5	38.5	8	80.0	23	74.2	36	66.7
Totals	13	24.1	10	18.5	31	57.4	54	

TABLE 10. Captains' estimate of the value of their vessels, in thousands of dollars, by place of residence. Percentages are of column totals. (Missing observations: 22.)

	Residence							
	Bristol Bay		Greater Alaska		Non-Alaska		Totals	
Value	No.	%	No.	%	No.	%	No.	%
≤10	10	83.3	1	12.5	2	8.0	13	28.9
11–20	1	8.3	1	12.5	8	32.0	10	22.2
21–40	1	8.3	2	25.0	11	44.0	14	31.1
>40	0	0.0	4	50.0	4	16.0	8	17.8
Totals	12	26.7	8	17.8	25	55.6	45	

TABLE 11. Opinion of respondents as to whether the limited entry system should be retained, repealed, or modified, by residence. Percentages are of column totals. (Missing observations: 9.)

	Residence							
	Bristol Bay		Greater Alaska		Non-Alaska		Totals	
Opinions	No.	%	No.	%	No.	%	No.	%
Retain in present form	4	7.3	5	41.7	15	40.5	24	23.1
Repeal—return to open entry	11	20.0	2	16.7	1	2.7	14	13.5
Modify present system	32	58.2	5	41.7	21	56.8	58	55.8
No opinion	8	14.5	0	0.0	0	0.0	8	7.7
Totals	55	52.9	12	11.5	37	35.6	104	

TABLE 12. Proposed modifications to limited entry by respondents who stated the system should be modified (Table 11), by residence. Respondents proposed one to three modifications. The question was open-ended. Percentages are of column totals.

	Residence							
	Bristol Bay		Greater Alaska		Non-Alaska		Totals	
Proposed modification	No.	%	No.	%	No.	%	No.	%
More permits for local fishermen	12	34.3	1	5.0	3	10.0	16	21.3
More permits for experienced fishermen	2	5.7	0	0.0	5	16.7	7	9.3
More enforcement	6	17.1	3	15.0	5	16.7	14	18.7
Halt issuance of further permits	1	2.9	2	10.0	4	13.3	7	9.3
End salability of permits	3	8.6	1	5.0	3	10.0	7	9.3
Control price	0	0.0	2	10.0	3	10.0	5	6.7
Other	11	31.4	1	5.0	7	23.3	19	25.3
Totals	35		10		30		75	

number of local residents (20%) but few nonlocal fishermen favored the direct repeal of the system (Table 12). Fishermen from the greater Alaska area and non-Alaskans generally held similar views concerning limited entry.

When asked the open-ended question, what aspects of the limited entry system they favored, nonlocal fishermen responded overwhelmingly that it limited competition (73%) and the amount of gear in the water (54%) (n = 48). Only 31 and 25% of Bristol Bay residents offered these responses, respectively (n = 59). Due to the higher fish prices in 1979

and improved harvests, it was generally felt that additional fishermen would enter the fishery if it were not for the permit system.

Whereas 41% of nonlocal fishermen felt limited entry had enhanced their income, only 4% of local residents felt the changed management had enhanced their family income; 49% of all village households surveyed responded that the system had actually diminished their income. When asked the open-ended question, what aspects, if any, of limited entry they were critical of, 58% of watershed residents responded that it inhibited the entry of young people into the fishery and, more generally, kept local people out of it. They tended to believe that an insufficient number of permits had been granted local residents initially, that permits were being further drained from the local area due to their sale, and that there was insufficient opportunity for young people to enter the fishery. These aspects of the Alaskan permit system are examined below.

In the survey of local villages, 22% of men over the age of 18 claimed that their application for a permit to fish in Bristol Bay had been denied. Of those denied a permit the median reported number of years fishing in Bristol Bay was 10 seasons (range, 2–33). In their own eyes and those of much of the community, most of these unsuccessful applicants are legitimate Bristol Bay fishermen. Why did they not qualify for permits?

Those watershed residents who were experienced fishermen and yet failed to obtain permits typically had not fished in the 2 yr just prior to the imposition of the limited entry system. The primary criterion used by the Alaskan Limited Entry Commission to determine status as a bona fide Bristol Bay fisherman was recent participation in the fishery as a license holder. Of 20 points required to obtain a permit, 3 points were allotted for each of the years 1971 and 1972 in which a license was held, 2 points each for 1969 and 1970, and 1 point for each year a license was held back to 1965. Dependence on the fishery for income was only considered for 1971–72 and 1972 was given greater weight. However, 1971–72 were off years for the fishery, 1972 being notably poor. Average net earnings per boat (before crew share) were $11 301 in 1970, $5538 in 1971, and $302 in 1972 (Langdon 1979 from Rogers and Kreinheder 1979). The expected runs are reasonably well-predicted in advance by Alaska Department of Fish and Game; the nature of the sockeye salmon cycle, which peaks every 5th yr in Bristol Bay (e.g. 1965/70) is also well-known by Bristol Bay fishermen. Bristol Bay residents are notably dependent upon seasonal income (Fig. 2), and some found alternate employment during those years. Some were engaged in training and employment on the Trans-Alaska pipeline project (Langdon 1979). Residents of Nondalton are often called upon to fight forest fires in the Alaskan interior. Although this occupation is highly subject to nature's vicissitudes, some found it worthwhile to wait at home for a fire call rather than fish during those years. Due to the generally cyclic nature of salmon runs (Ricker 1950), economic pluralism became a viable strategy for many local rural residents. However, many who did not fish the poor years were later unable to obtain a permit.

The relationships between fishermen on a vessel tended to differ between local and nonlocal fishermen. Proportionately, almost three times as many local residents fished as full partners rather than in a captain–crew relationship (33% vs. 12%; $\chi^2 = 2.80$, df = 1, $P < 0.10$). In these instances, the vessel and gear were jointly owned, and all fishing costs and income were shared equally. In the prelimited entry era, only one man could hold the fishing license, but this was a formality as the license conferred no privilege. However, this predominantly rural fishing relationship was not recognized by the Limited Entry Commission. Points sufficient to obtain a limited entry permit were based upon the years as *license holder*. Thus, only one partner could receive a permit; today, if the partnership dissolves, only the permit holder is assured of being able to continue fishing.

Other aspects of the permit application also appear based upon a nonrural definition of a legitimate fisherman. Points were awarded for fishing more than 3 wk during each of the 1971 and 1972 seasons. However, the Bristol Bay sockeye run is often largely completed in ~10 d, although processors promote "professionalism" among the fishermen to have sufficient fishermen to harvest the tails of the run. Local residents have been noted historically to fish predominantly during the peaks of the runs (Rogers 1972), because they depend upon subsistence activities to support their families. Imported foods are highly expensive in these isolated regions, so considerable numbers of salmon are salted, dried and smoked, and canned for the winter. The activity is labor intensive, so local fishermen may return to their villages from Naknek in less than 3 wk, particularly during years of poor commercial fishing, such as 1971–72. Thus this aspect of the application further discriminated against local residents.

Local residents noted several other factors that may have contributed to their inadequate representation in the fishery. Many reported difficulty in understanding the application form, which was long and complex. The original application contained seven pages (four forms) and was accompanied by 41 pages of instructions. To obtain points for various sections required records of gear and vessel ownership, of past years' fishing activity and earnings, and computation of percentage income derived from the Bristol Bay fishery. In 1970, the median number of years of schooling received by Bristol Bay Natives over 25 yr of age was 3.9 yr; 21% of this population had received no formal education; 79% had not gone beyond the elementary level (grade 8) (Langdon 1979). Many did not maintain adequate records for documentation, and the degree to which affidavits were accepted is unclear. Although assistance was provided in filling out the permit applications, many residents questioned the competence and degree of interest of the counsellors. This allegation is supported by the Alaska Legal Services Corporation, which instituted a lawsuit against the Limited Entry Commission on grounds that application assistance was insufficient (Adasiak 1979).

Despite numerous appeals of permit applications, lawsuits (Adasiak 1979), hearings at local and state level, and reports (Koslow 1979; Langdon 1979, 1980) in which these aspects of the Alaskan limited entry program have been raised, the Limited Entry Commission has shown little sign of yielding to pressure from the rural population. Of 30 appeals of permit applications encountered on the village surveys, only 1 had been successful. According to respondents, eight (27%) remained outstanding despite the passing of the fishing season. Although the legitimacy of these claims could not be judged, it may be noted that the single successful appeal followed a

TABLE 13. Probabilities (χ^2 tests, df = 1) of family involvement in fishing.

	Native vs. all other	Native + European ethnic vs. all other	Local vs. all nonlocal	Bristol Bay + non-Alaskan vs. greater Alaskan
Crewed with immediate family	NS	NS	0.025	<0.01
Crewed with non-immediate family	<0.25	NS	<0.01	NS
Present crew: A relation	NS	<0.025	NS	<0.05

TABLE 14. Response to question, "Do you want your son(s) to be a fisherman?" (Missing observations: 7.)

Response	Residence			
	Bristol Bay	Greater Alaska	Non-Alaska	
Yes	7	2	6	
No	0	1	7	
It is up to him	6	2	2	
Want him to fish: not to be a fisherman	0	1	1	
Without sons	1	4	15	
Totals	14	10	33	60

costly, time-consuming, and aggressive campaign by one of the better educated residents (a health aide).

The free transferability of permits under the Alaska limited entry system has led to a substantial drain of permits from the Bristol Bay area. Between 1975 and 1979, permit transfers resulted in the net loss of 43 permits from local residents to non-Alaskans and residents of greater Alaska. This represented 6% of the original permits issued to local residents (Table 1) (Langdon 1980). Residents reported that permits were often sold in winter in times of need during the poor salmon years. Furthermore, because local residents earn less from the fishery than nonlocal fishermen, local fishermen tend to devalue the permit relative to nonlocal fishermen (Langdon 1980). Due to recent good salmon harvests, the average purchase price of a permit rose from $1166 in 1975 to $69 667 in 1979 (Langdon 1980). Given the extremely limited means of local residents, the drain of permits from the local area appears to be increasing (Langdon 1980).

Perhaps the most significant impact of limited entry upon the local villages results from the way it transforms the transmission of the fishery to future generations. Although family ties are an important component of the social fabric of all fishery groups, they are particularly pervasive among local Native-Alaskan and non-Alaskan European ethnic fishermen. Fishing captains from these groups generally showed a greater tendency to have crewed themselves with family and relatives and to have their relations presently serving as crew (Table 13). (The typical Bristol Bay gill-netter is fished by the captain and a single crewmember.) Seventy-one percent of Native and European ethnic fishermen had family and relatives presently serving as crew compared with 40% on other vessels. Entry into the fishery has traditionally followed family lines in these groups, young men receiving training as crewmembers with relatives until they are prepared to acquire their own vessel. However, under the present limited entry system, only one member of a family may attain status as an independent fisherman, and then only upon the permitholder's retirement, if the permit is transmitted along family lines.

Because this change would seem to affect all traditional fishery groups (in this fishery, local Native fishermen and non-Alaskan European ethnic fishermen in particular) the question arises why these two groups viewed the limited entry system so differently. For one, rural Native-Alaskans have notably large families, so the pressure for permits is particularly great. In 1970, the modal family size for this population was 7 and the mean was 5.7, compared with the non-Native-Alaskan modal family size of 2 and mean of 3.7 (Langdon 1979). The village survey indicated that although two-thirds of men 18–35 fished in Bristol Bay, 72% in this group had no permit. The situation is particularly severe among the younger men: 85% of those surveyed between 18 and 24 yr of age had no permit. The ability to attain independent status within the fishery appears effectively closed to a large proportion of the rural fishing population, given the large proportion of young within this group and the shrinking number of permits held locally. Furthermore, discussions indicated that the families of many non-Alaskan European ethnic fishermen appeared to be undergoing acculturation. Many of their children were embarked upon nonfishing, often college-based, careers. Rural Alaskans, on the other hand, generally lack alternate opportunities due to limitations of regional economies and lack of education and skills to compete in the urban environment. Thus locally resident fishing captains who held a preference as to their son(s)' career were virtually unanimous in their desire for them to fish. Nonlocal fishing captains, regardless of residence or ethnicity, were divided, as many preferring their sons to take up another career as want-

ing their sons to be fishermen (Table 14).

Discussion

In examining the impact of limited entry policy among the different fishery groups in Bristol Bay, a clear dichotomy was found between local and nonlocal fishermen. Nonlocal fishermen were generally well-equipped and able to realize any increased rent due to limited entry, i.e. a rate of return above that which would accrue to an open entry fishery. On the other hand, local rural communities appeared to suffer under the present system. Initially, some local residents of longstanding experience fishing and who considered themselves legitimate Bristol Bay fishermen were unable to obtain permits. The permit application made apparent allowance for local fishermen by awarding points for rural residence and degree of dependence upon the fishery, although, for the latter, only during 1971–72. However, the application's implicit definition of a legitimate Bristol Bay fisherman was based upon the nonrural fisherman, one who fishes every season, good or bad, and fishes the entire season, both the peak and tails of the run, and who maintains written records of income and has sufficient education to comprehend a complex application process. The application failed to recognize the need of local rural residents to maintain a diversified economy in the face of the drastically fluctuating salmon runs. These conflicting tendencies within the permit application created apparent anomalies: permits were received by some fishermen who first skippered only several seasons prior to the institution of limited entry, while longstanding Bristol Bay fishermen who went elsewhere during those years were denied further access to the fishery.

From 1975 to 1979, 6% of permits issued to Bristol Bay residents has been transferred to nonlocal fishermen (Table 1). The Limited Entry Commission has denied that this has been a problem based upon preliminary findings in southeast Alaska (Adasiak 1979). However, Langdon (1980) analyzed permit transfers in all Alaskan limited entry fisheries over the period 1975–79 and found a net loss of 3.5% of permits from local rural Alaskan fishermen due to transfers. A similar pattern was found earlier when limited entry was instituted in Canadian Pacific salmon fisheries. Ultimately, Canada instituted an alternate nontransferable permit for local Native fishermen (Campbell 1973). This pattern seems based upon the poorer earnings of rural fishermen, which causes them to devalue the permit relative to other fishermen, and their more severe short-term exigencies due to greater dependence for cash upon the fluctuating salmon harvest.

However, the most significant impact of the Alaskan limited entry program upon local fishing communities may prove to be the severe limitation it places upon entry into the fishery of the burgeoning youthful rural population. This situation would not be critical if other local opportunities were expanding or if out-migration were a viable alternative. However, based upon the 1970 census, Kresge et al. (1977) found that only 31% of Natives 14 yr of age and older were employed, less than half the proportion of white Alaskans. Eighteen percent of Natives actively seeking employment were unable to find jobs, and of those who were employed, over half worked for 26 wk of the year or less. Mean per capita income of Native Alaskans was one-third that of white Alaskans. Although increasing numbers of Natives are enrolling in college, the success rate is half that of non-Native students, and overall numbers graduating are very low; in 1969–72, an average of 22 Natives per year received a 4-yr college degree (Kohout and Kleinfeld 1974), although Native groups compose 20% of the Alaskan population.

Certain aspects of the local situation could not be quantified, but are nonetheless important. Five years after the institution of limited entry, the author found a prevailing mood of bitterness and frustration among Bristol Bay residents. Some consider access to the resource an aboriginal right. Many expressed the view that the program had been originally proposed to them as a means to prevent the fishery from being taken over by "outsiders," but that it had resulted in closure of the fishery to themselves. This mood is enhanced by the apparent unresponsiveness of the Commission and state government to their situation despite numerous appeals, lawsuits, hearings, and promises by political leaders. Apparently without recourse through legitimate channels and without opportunity either in the village or the outside world, there appeared to be widespread illegal fishing (i.e. fishing without permits), despite the risk of a high fine. Many fishermen spoke of the need for more enforcement (Table 12). To maintain credibility, the system must be enforced. However, under present circumstances, violation of the system serves as a safety valve to relieve the pressures caused by its inequities.

In response to criticism, the state of Alaska expanded a loan program in 1978 to enable Alaskan residents to buy permits. However, the application is again relatively complex and its requirements for information and collateral may appear prohibitive to rural Alaskans. Preliminary analysis by Langdon (1980) indicated successful loan applicants were primarily from urban Alaska, and there was little impact upon local rural communities. In Bristol Bay, three local residents and eight nonlocal urban Alaskan residents had successfully obtained permit loans 1 yr after initiation of the program.

If the Alaskan limited entry system is to enhance the state's rural economy, some aspect of the program must be directed more clearly to inclusion of that segment of the society. Economic revitalization might begin with issuance of nontransferrable permits to rural residents of coastal or watershed regions with greater than, say, 5 yr of fishing experience. A state loan program directed specifically to rural Alaskans for purchase of adequate vessels and gear, as well as permits, would enable rural Alaskans to achieve parity with nonlocal fishermen. Although the change would be politically difficult at this time, the system should be based upon a nontransferable permit, so that as fishermen retired, new fishermen could enter based upon equitable criteria (e.g. experience in the fishery and dependence upon it).

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Influence of Time and Size at Release of Juvenile Coho Salmon (*Oncorhynchus kisutch*) on Returns at Maturity

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BILTON, H. T., D. F. ALDERDICE, AND J. T. SCHNUTE. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Can. J. Fish. Aquat. Sci. 39: 426–447.

Juvenile coho salmon (*Oncorhynchus kisutch*) were raised in six ponds at Rosewall Creek, Vancouver Island, British Columbia, from which releases were made at four times: April 14, May 12, June 10 and July 8, 1975. Prior to each release a portion of the juveniles in each pond were graded into three size groups (small, medium, large) based on size distributions in each pond. The juveniles were nose-tagged according to size group, pond, and release date, and marked by adipose fin removal. A total of 57 groups were released. Returns of adults and precocious males (jacks) to the weir and to the fishery (commerical, sport) were subjected to response surface analysis. Maximum adult returns of 43.5%, to the weir and fishery, were predicted for release of 25.1-g coho juveniles on the 173rd (Julian) day from January 1 (June 22, 1975). A significant interaction was noted between release time and size: maximum returns from early (April 14) releases would be expected from release of 16- to 17-g juveniles. Returns of jacks from the six ponds ranged from 0.0 to 4.65%. Predicted returns of jacks would be maximized from early release of large juveniles (>~20 g in April). The benefit–cost ratio at the center of the time and size of release surface for maximum adult returns was estimated as 12.2:1. Maximum benefit–cost ratios were calculated for release of smaller juveniles between June 17 and 22, 1975. Benefit–costs associated with releases on the path of joint optimality between the two response centers rose from 12.2:1 (maximum adult returns) to a calculated 16.5:1 for release of 7.5-g juveniles on June 17, 1975. Size and time at juvenile release and success of adult returns are viewed as initial and final aspects of a biological system whose central components as yet are imperfectly understood. Some parts of the system are discussed in relation to possible ways of increasing the efficiency and cost–effectiveness of salmonid hatchery technology, as well as in predicting the success of returns in relation to conditions influencing survival and growth of juvenile migrants from natural stocks.

Key words: coho salmon, juvenile salmon, release time and size, response surface analysis and optimization, survival, biomass, benefit–costs

BILTON, H. T., D. F. ALDERDICE, AND J. T. SCHNUTE. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Can. J. Fish. Aquat. Sci. 39: 426–427.

Des jeunes saumons coho (*Oncorhynchus kisutch*) ont été élevés dans six étangs à Rosewall Creek, île Vancouver (Colombie-Britannique). Ils furent libérés à cet endroit à quatre occasions : 14 avril, 12 mai, 10 juin et 8 juillet 1975. Avant chaque mise en liberté, un certain nombre de chaque étang furent classés en trois groupes (petits, moyens et grands) selon la distribution des tailles dans chaque étang. On fixa une étiquette sur le nez selon la taille, l'étang et la date de mise en liberté, et on les marqua par ablation de la nageoire adipeuse. Un total de 57 groupes furent ainsi libérés. Les retours d'adultes et de mâles précoces (« jacks ») dans les parcs et les pêches (commerciale, sportive) furent soumis à une analyse de surface de réponse. Le plus haut pourcentage de retours d'adultes, soit 43,5 %, devait se produire, d'après les prédictions applicables aux poissons de 25,1 g, au 173^{e} jour (julien) à partir du 1er janvier (le 22 juin 1975). Nous avons observé une interaction significative entre le moment de mise en liberté et la taille : on pourrait s'attendre que les retours les plus nombreux de poissons mis en liberté de bonne heure (14 avril) se produiraient avec les jeunes de 16–17 g. Les retours de « jacks » des six étangs ont varié de 0,0 à 4,65 %. En libérant tôt des juvéniles de plus grande taille (>~ 20 g en avril) on maximiserait les retours prédits des « jacks ». On a estimé à 12,2:1 le rapport coûts–bénéfices au point médian du

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temps et de la taille de la surface de mise en liberté pour des retours d'adultes maxima. Les rapports coûts−bénéfices maxima ont été calculés dans le cas de mise en liberté de juvéniles de petite taille entre les 17 et 22 juin 1975. Les coûts−bénéfices associés avec les mises en liberté sur la voie d'une optimalité conjointe entre les deux centres de réponse passa de 12,2:1 (retours d'adultes maxima) à un rapport calculé de 16,5:1 avec la libération de jeunes de 7,5 g le 17 juin 1975. Nous envisageons la taille et le moment de mise en liberté des juvéniles et la réussite des retours d'adultes comme les aspects initial et final d'un système biologique dont les éléments centraux sont encore mal compris. Nous analysons certaines parties du système en relation avec des méthodes susceptibles d'accroître le rendement et le coût−efficacité de la technologie des établissements d'élevage des saumons et permettant de prédire le succès des retours par rapport aux conditions influençant la survie et la croissance des migrants juvéniles de stocks naturels.

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UNDER a federal−provincial Salmonid Enhancement Program, efforts are being made to increase British Columbia salmonid stocks. One strategy being employed is to seek ways for improving the biological effectiveness of existing and proposed salmonid hatcheries. An associated tactical approach to this objective has involved examination of the influence of size of juvenile salmon and the time of their release on their subsequent return as mature fish. Evidence obtained by American salmonid hatcheries on the Pacific Coast indicates that survival of juvenile coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon can be influenced by the size of smolts at release (Wallis 1968; Johnson 1970; Hopley and Mathews 1975; Hager and Noble 1976). The study by Hopley and Mathews (1975) indicated that both time and size at release of yearling coho influenced the survival and the size of returning adults, those fish maturing in their 3rd yr of life.

The objective of the experiment reported here was to determine the simultaneous effects of both time and size at release of juvenile coho salmon on their subsequent survival, growth, and age at maturity. A number of supporting details of the study, including escapement and catch data, have been reported elsewhere (Bilton 1978, 1980). This paper, based on the data from the earlier reports, uses response surface analysis to compute those conditions of release that maximize the numbers and biomass of returning adults. In doing so, it examines the contribution of the various experimental release groups in terms of percent survival and biomass of returning adults and jacks (precocious males maturing as 2-yr-olds). It also examines benefit−cost ratios for returning fish in relation to time and size at juvenile release. Because the response surface centers associated with percent return, biomass, or benefit−cost ratios would not necessarily coincide, a further analysis describes alternative time and size of release conditions in terms of efficiency of return and associated benefit−cost ratios. These conditions are described on a path of joint optimality lying between the response centers for maximum percent return and maximum benefit−costs.

Experimental Methods

LOCATION, STOCK, AND REARING

The experiment was carried out at Rosewall Creek hatchery, Vancouver Island, B.C., which is operated by the Pacific Biological Station, Nanaimo, B.C. (Fig. 1). Rosewall Creek is located ~80 km north of Nanaimo on the east coast of Vancouver Island, and flows into Georgia Strait.

The coho eggs used were from the Big Qualicum River, ~24 km south of Rosewall Creek. A total of 200 thousand eggs were taken, fertilized, and incubated to the "eyed" stage at the Big Qualicum hatchery. The eyed eggs were transferred to the Rosewall Creek hatchery and incubated in well water at temperatures of 6−7°C.

The resulting fry were divided equally into six groups and moved into six Burrows ponds. Throughout rearing, the fish were fed Oregon Moist Pellets (OMP) from automatic feeders every 15 min daily during daylight hours. Water temperatures were partially controlled using Rosewall Creek water or groundwater, separately or mixed.

EXPERIMENTAL DESIGN

Initially it was planned (1) to rear three populations of juvenile coho to three successively larger mean sizes by manipulating water temperature; (2) to replicate each of the three populations once, making a total of six populations; (3) to release one-third of each of the six populations at three different times, in April, May, and June; and (4) to compare the returns from each release. However, this plan was not achieved; temperature differences in the two available water supplies were not sufficient to provide the required differences in growth rate. The six ponds in Table 1 refer to the six original experimental populations. Average water temperature of ponds 1 and 4, set up to provide "small" fish, was only 2.3°C lower than that of ponds 2 and 5, set up to provide "medium-sized" fish. Average water temperature of the latter ponds was 0.2°C lower than that of ponds 3 and 6, set up to provide "large" fish. By the time of the first proposed release, only a small difference (1.2 g) was evident between the average weights of the medium (ponds 2, 5) and large (ponds 3, 6) fish. Therefore, to achieve larger differences in size among the groups of juveniles, we graded the fish in each of the six pond populations into three size groups (S, small; M, medium; L, large) prior to tagging (Table 1). Hence the original design, involving populations of fish of different sizes replicated between ponds, was abandoned in favor of providing graded size groups in the populations within ponds. The size groups selected were based on preliminary sampling for length distribution of fish in each population. The middle

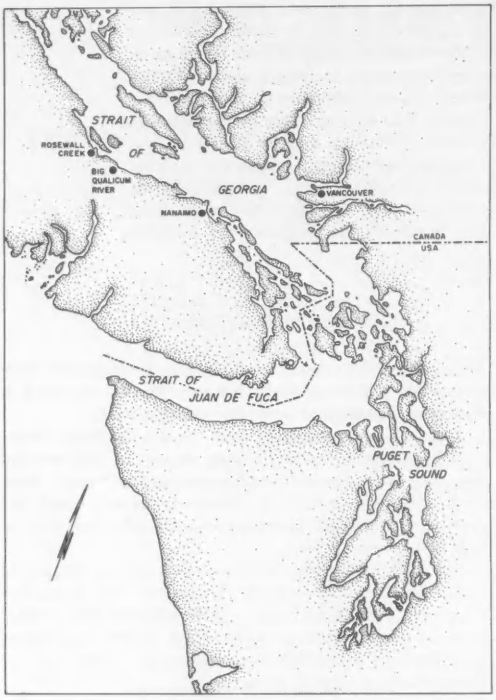

FIG. 1. Locations and geographic features mentioned in the text.

portion of the distributions, constituting 50% of the sample, provided the range for medium-sized fish. Those below and above the midrange, comprising 25% of the sample in each group, were classed as small and large, respectively. The potential genetic bias introduced by grading is considered later in the analysis.

A fourth release of juveniles was made in July using the combined excess fish from the six ponds. In this instance, three size groups were tagged and released from the single population. These and the groups previously released provided a total of 57 individually tagged groups. That is, three size groups were liberated from each of the six ponds in each of the first three releases plus the three groups making up the last release (Table 1).

The number of smolts making up each of the three size groups from the six populations at each release time ranged as follows:

Release	Small	Medium	Large
April 14	1243–1788	3585–3867	1657–1787
May 12	1830–1888	3639–3784	1839–1909
June 10	878–1642	1853–3937	1172–1898
July 8	1432	3704	1801

Fish in each of the 57 groups released were tagged several weeks prior to release using coded wire nose tags. A specific tag code identified each release group, and all tagged fish were marked, for later recognition, by removal of the adipose fin. At the time of each release a sample of fish was obtained. These fish were sacrificed and individuals were sampled for length, weight, scales, and percent nose tag retention. These data provided estimates of size distribution and sex ratio in each release group.

RECOVERY OF JACKS AND ADULTS

Jack coho salmon (age 1.0[1]) were recovered from Rosewall Creek in the fall of 1975, and adults (age 1.1[1]) in the fall of 1976. Marked fish, those with a missing adipose fin, were captured in a trap adjacent to the release ponds, located immediately downstream from an electric fence. Approximately 200 unmarked fish, assumed to be wild fish or fish that had escaped from the hatchery, were transferred alive upstream above the fence. All marked jacks and adults were sacrificed and sampled (fork length (cm), weight (g), sex, scale samples). The heads were removed, frozen, and retained for subsequent recovery of the nose tags. The returning fish were assigned to their appropriate release groups after inspection of the recovered tags.

Nose-tagged coho also were recovered from the commercial net and troll fisheries by random sampling of catches at a target intensity of 20% (Heizer et al. 1978). Estimates of numbers of fish caught from each tag group were obtained on the basis of the actual number of tagged fish recovered from the fisheries, the sampling effort, and the marked-to-unmarked ratio in the catches (Bilton 1980).

In addition, returns of tagged coho from sport catches were obtained through the Georgia Strait head recovery program (Argue et al. 1977). This program depends on voluntary return of heads from marked chinook and coho salmon by Georgia Strait and Strait of Juan de Fuca sport fishermen. To estimate the total number of tagged Rosewall Creek coho that contributed to the sport fishery we assumed that 28% of tagged fish caught would be recognized and reported. This "awareness factor," based on a number of values not directly measured, was assigned a value on the basis of area-by-area comparison with Puget Sound fisheries (Argue et al. 1977), and use of Puget Sound awareness factors for 1974 (Kimura 1976). Assumed Georgia Straight values can be referred to as Puget Sound equivalent awareness factors.

DATA COMPILATION

Percent return of mature fish — Total returns from the 57 groups of juveniles released were determined, as indicated, from the number of returning jacks and adults in the escapement and the numbers estimated to have been caught in the commercial and sport fisheries. Percent return, for each release group, was derived from the number of jacks and adults recovered in relation to the number of juveniles released (Table 1). The numbers of jacks and adults recovered

[1]The European system of age designation (Koo 1962) is used in this report. The first digit indicates the number of annuli formed in fresh water and the second digit the number of annuli formed in the ocean. Hence a 1.0-fish returns in its 2nd yr (from hatching) after spending 1 yr in freshwater and part of 1 yr in the ocean. A 1.1-fish returns in its 3rd yr after spending 1+ yr in the ocean.

TABLE 1. Release and return data for tagged juvenile coho liberated from the original six pond populations, each population graded into three size groups: S, small; M, medium; L, large (see text). The four entries under each pond and size group represent, respectively: average juvenile weight (g) at release, percent return of adults, of jacks, and total return (adults plus jacks). Release dates, in Julian days, refer to the number of days elapsed from January 1, 1975.

Release date 1975	Size group	Pond populations					
		Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6
April 14	S	5.1 g	9.0 g	9.2 g	7.0 g	9.6 g	10.6 g
(Julian day		11.58	3.13	7.44	10.00	8.76	9.46
104)		0.08	0.12	0.00	0.00	0.21	0.11
		11.66	3.25	7.44	10.00	8.97	9.57
	M	8.1 g	11.6 g	12.9 g	9.6 g	12.6 g	14.2 g
		8.40	7.16	9.49	9.02	5.08	6.23
		0.08	0.21	0.25	0.19	0.08	0.14
		8.48	7.37	9.74	9.21	5.16	6.37
	L	10.9 g	15.4 g	16.1 g	13.3 g	16.7 g	18.8 g
		8.47	7.66	4.42	5.99	4.43	3.94
		0.34	0.30	0.62	0.17	0.96	0.62
		8.81	7.96	5.04	6.16	5.39	4.56
May 12	S	8.3 g	12.5 g	11.7 g	7.7 g	13.8 g	14.0 g
(day 132)		15.91	15.98	13.83	16.00	12.39	19.02
		0.16	0.32	0.32	0.00	0.70	0.87
		16.07	16.30	14.15	16.00	13.09	19.89
	M	11.9 g	15.7 g	15.1 g	11.0 g	18.1 g	18.5 g
		14.65	18.67	17.62	16.65	15.54	16.47
		0.55	1.49	0.75	0.42	2.42	2.42
		15.20	20.16	18.37	17.07	17.96	18.89
	L	15.1 g	20. 8 g	19.2 g	15.3 g	23.9 g	25.8 g
		13.61	15.77	12.48	17.28	13.72	15.66
		1.49	4.19	3.55	1.17	3.66	5.00
		15.10	19.96	16.03	18.45	17.38	20.66
June 10	S	12.3 g	15.6 g	14.4 g	12.3 g	17.3 g	17.6 g
(day 161)		32.71	34.53	24.74	32.69	29.99	36.44
		0.00	0.24	0.07	0.11	0.07	0.25
		32.71	34.77	24.81	32.80	30.06	36.69
	M	16.0 g	20.1 g	18.9 g	16.3 g	22.1 g	23.6 g
		37.63	41.40	39.77	40.26	38.57	42.03
		0.54	0.89	0.83	0.49	1.36	1.26
		38.17	42.29	40.60	40.75	39.93	43.29
	L	20.2 g	28.3 g	25.1 g	19.9 g	28.7 g	31.8 g
		38.21	31.80	38.36	43.34	30.30	30.80
		2.67	4.48	5.00	2.15	6.16	7.42
		40.88	36.36	43.36	45.49	36.46	38.22
July 8	S	14.9 g					
(day 189)		4.82					
		0.00					
		4.82					
	M	24.8 g					
		20.17					
		0.97					
		21.14					
	L	33.1 g					
		13.71					
		3.05					
		16.76					

in the escapement are highly reliable as it was possible to examine all fish in the escapement. Estimates of numbers of fish caught by the commercial fishery are considered reasonable but less certain. They arise from a consistent sampling effort carried out routinely in most commercial fishing areas over the fishing season, from which good estimates of the catches and marked-to-unmarked ratios were obtained. However, estimates of numbers of fish caught by the sport fishery (Bilton 1980) are considered lower in reliability. More recent evidence suggests the awareness factor for northern Georgia Strait (Fig. 1), an area adjoining the release location, may have been substantially lower than the equivalent Puget Sound awareness factor we used. Hence estimates of numbers of tagged coho caught by the sport fishery, as used herein,

TABLE 2. Release and return data for tagged juvenile coho liberated from six pond populations, each population graded into three size groups: S, small; M, medium; L, large (see text). The four entries under each pond and size group represent, respectively: average juvenile weight (g) at release, and biomass of adults, of jacks, and total biomass (adults plus jacks). Biomass (thousands of pounds) is based on pounds of returning fish per 100 000 juveniles released. Release dates, in Julian days, refer to the number of days elapsed from January 1, 1975.

Release date 1975	Size group	Pond populations					
		Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6
April 14	S	5.1 g	9.0 g	9.2 g	7.0 g	9.6 g	10.6 g
(Julian day		55.71	23.17	43.09	54.77	45.82	53.79
104)		0.08	0.13	0.00	0.00	0.30	0.16
		55.79	23.30	43.09	54.77	46.12	53.95
	M	8.1 g	11.6 g	12.9 g	9.6 g	12.6 g	14.2 g
		49.33	42.89	50.61	47.23	28.81	44.81
		0.08	0.22	0.28	0.16	0.12	0.19
		49.41	43.11	50.89	47.39	28.93	45.00
	L	10.9 g	15.4 g	16.1 g	13.3 g	16.7 g	18.8 g
		57.31	49.45	21.33	32.36	30.73	28.24
		0.36	0.32	0.70	0.14	1.34	0.85
		57.67	49.77	22.03	32.50	32.07	29.09
May 12	S	8.3 g	12.5 g	11.7 g	7.7 g	13.8 g	14.0 g
(day 132)		88.41	100.90	84.65	84.97	78.52	117.33
		0.14	0.37	0.37	0.00	0.88	0.98
		88.55	101.27	85.02	84.97	79.40	118.31
	M	11.9 g	15.7 g	15.1 g	11.0 g	18.1 g	18.5 g
		88.24	120.70	106.93	94.36	101.36	110.50
		0.49	1.70	0.87	0.37	2.88	3.01
		88.73	122.40	107.80	94.73	104.24	113.51
	L	15.1 g	20.8 g	19.2 g	15.3 g	23.9 g	25.8 g
		78.65	113.50	81.12	102.55	97.01	107.06
		1.51	5.05	4.61	1.11	4.71	6.36
		80.16	118.55	85.73	103.66	101.72	113.42
June 10	S	12.3 g	15.6 g	14.4 g	12.3 g	17.3 g	17.6 g
(day 161)		161.82	173.45	131.19	151.78	147.40	199.50
		0.00	0.20	0.06	0.08	0.06	0.20
		161.82	173.65	131.25	151.86	147.46	199.70
	M	16.0 g	20.1 g	18.9 g	16.3 g	22.1 g	23.6 g
		185.71	214.06	205.79	201.51	206.58	226.38
		0.42	0.72	0.72	0.34	1.16	1.04
		186.13	214.78	206.51	201.85	207.74	227.42
	L	20.2 g	28.3 g	25.1 g	19.9 g	28.7 g	31.8 g
		199.75	179.00	211.77	216.11	163.43	169.42
		1.93	3.67	4.25	1.65	5.30	6.19
		201.68	182.67	216.02	217.76	168.73	175.61
July 8	S	14.9 g					
(day 189)		21.0					
		0.00					
		21.10					
	M	24.8 g					
		88.32					
		0.55					
		88.87					
	L	33.1 g					
		61.38					
		1.79					
		63.17					

probably are conservative.

Biomass of mature fish returns — Estimates of biomass of returning fish from each of the 57 release groups (Table 2) were computed as thousands of pounds (1 kg = 2.2 lb) per 100 000 juveniles released. These estimates are based on (1) rate of return of jacks and adults from the 57 release groups (Table 1); (2) proportionally, the numbers that would have returned if 100 000 juveniles had been released in each of the 57 groups; and (3) the final average weight of jacks and of adults for each of the release groups sampled in the escapement. The latter calculation uses the weight of fish returning to the fence as a standard. It would be unbiased if none of the fish were caught in the fishery, and all were free to return to the hatchery. The estimated biomass of jacks originating from

TABLE 3. Release and return data for tagged juvenile coho liberated from six pond populations, each population graded into three size groups: S, small; M, medium; L, large (see text). The four entries under each pond and size group represent, respectively: average juvenile weight (g) at release, and benefit–cost ratios for returns of adults, of jacks, and for total returns (adults plus jacks). Benefit–cost ratios are based on the value of returns ($Can/lb) relative to production costs ($Can/100 000 juveniles) to time of release. Release dates, in Julian days, refer to the number of days elapsed from January 1, 1975.

Release date 1975	Size group	Pond populations					
		Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6
April 14	S	5.1 g	9.0 g	9.2 g	7.0 g	9.6 g	10.6 g
(Julian day		9.569	2.255	4.103	6.854	4.181	4.446
104)		0.014	0.013	0.000	0.000	0.027	0.013
		9.583	2.268	4.103	6.854	4.208	4.459
	M	8.1 g	11.6 g	12.9 g	9.6 g	12.6 g	14.2 g
		5.336	3.239	3.437	4.310	2.003	2.765
		0.009	0.016	0.019	0.015	0.008	0.012
		5.345	3.255	3.456	4.325	2.011	2.777
	L	10.9 g	15.4 g	16.1 g	13.3 g	16.7 g	18.8 g
		4.606	2.813	1.161	2.131	1.612	1.316
		0.029	0.018	0.038	0.009	0.070	0.040
		4.635	2.831	1.199	2.140	1.682	1.356
May 12	S	8.3 g	12.5 g	11.7 g	7.7 g	13.8 g	14.0 g
(day 132)		11.383	8.627	7.732	11.793	6.081	8.956
		0.019	0.031	0.034	0.000	0.068	0.075
		11.402	8.658	7.766	11.793	6.149	9.031
	M	11.9 g	15.7 g	15.1 g	11.0 g	18.1 g	18.5 g
		7.925	8.216	7.568	9.168	5.985	6.383
		0.044	0.116	0.061	0.036	0.170	0.174
		7.969	8.332	7.629	9.204	6.155	6.557
	L	15.1 g	20.8 g	19.2 g	15.3 g	23.9 g	25.8 g
		5.566	5.832	4.515	7.163	4.334	4.435
		0.107	0.259	0.256	0.078	0.211	0.264
		5.673	6.091	4.771	7.241	4.545	4.699
June 10	S	12.3 g	15.6 g	14.4 g	12.3 g	17.3 g	17.6 g
(day 161)		17.325	14.642	11.998	16.250	11.220	14.927
		0.000	0.016	0.006	0.009	0.004	0.015
		17.325	14.658	12.004	16.259	11.224	14.942
	M	16.0 g	20.1 g	18.9 g	16.3 g	22.1 g	23.6 g
		15.285	14.024	14.339	16.280	12.309	12.632
		0.035	0.047	0.050	0.028	0.069	0.058
		15.320	14.071	14.389	16.308	12.378	12.690
	L	20.2 g	28.3 g	25.1 g	19.9 g	28.7 g	31.8 g
		13.022	8.329	11.110	14.301	7.499	7.016
		0.126	0.171	0.223	0.109	0.243	0.256
		13.148	8.500	11.333	14.410	7.742	7.272
July 8	S	14.9 g					
(day 189)		2.165					
		0.000					
		2.165					
	M	24.8 g					
		5.445					
		0.034					
		5.479					
	L	33.1 g					
		2.835					
		0.083					
		2.918					

each release group is considered highly reliable as virtually all are considered to have been recovered. Only small numbers of jacks were estimated to have been taken by the fishery in the year of release; estimates ranged from 4 to 83 fish for the various release groups (Bilton 1980). On the other hand, final average weight of the adults escaping to the fence likely overestimates the biomass of adults actually produced from each release group. Weights of adults taken in the fishery would have been lower, particularly for those fish caught early in the season when the fish would be smaller.

Benefit–cost ratios — Estimated benefit–cost ratios for returning jacks and adult coho were calculated for the value

of returns relative to the costs incurred in rearing the fish at the experimental hatchery (Table 3). A simplified benefit–cost relation is used; its main function is to provide a relative comparison of returns among the 57 tagged groups released. Estimates of benefit or value were derived as follows: (1) from the escapement, estimates were obtained of the expected biomass (per 100 000 juveniles released) of returning adults and jacks from each release group (Table 2); (2) the returning poundage of adults and jacks was assigned a single value of $0.90 Can./lb at the hatchery weir. Hence, benefits were calculated by multiplying the poundage of adults or jacks by the single rate of $0.90/lb. These estimates of benefit are conservative, underestimating the true value of returns taken by the commercial and sport fisheries.

Estimates of production costs at the experimental hatchery were derived as follows: (1) costs per pound of juveniles reared, excluding capital costs, were accumulated to each release date; (2) the estimated weight per 100 000 juveniles was computed from the mean juvenile weights for each release group. From these figures the noncapital operating costs of production were estimated (Bilton and Jenkinson 1976) to be $4.66 Can. (per pound) for the April release, $3.82 for May, $3.10 for June, and $2.67 for July. Over the total period of culture there was an increase per fish in the cost of rearing. However, this increase was offset by higher food conversion efficiency in the latter months of culture so that the cost of production per pound of juveniles declined between the first and final releases. The estimates of cost, based on releases from an experimental hatchery, may not truly represent the costs incurred in a production hatchery. However, discussions with production hatchery personnel suggest the estimates presented here are not unreasonable.

The benefit–cost ratios were derived through division of the calculated benefits by the estimated production costs. For example, for every dollar spent in producing 5.1-g juveniles for release in April there was a yield of $9.57 Can. in terms of adult flesh produced (Table 3). The estimates of value per pound of adult flesh produced are considerably lower than the true value realized by the fisheries. Hence the benefit–cost ratios, calculated from these data, must be viewed as conservative in absolute value.

Analytical Methods

Response Surface Methods

The design and results of the entire experiment are summarized in Tables 1–3. For each of the 57 releases, the (Julian) release date, x_1, is shown along with mean juvenile weight at release, x_2, in grams. These two variables are considered control variables; potentially they may be controlled, at least to some extent, in the hatchery. Nine possible responses to these controls are listed (Table 4), as measured in this experiment.

Sophisticated analysis hardly is necessary to prove that manipulating time and size at release (x_1, x_2) has an effect on the responses y_j ($j = 1, 2, \ldots, 9$). For example consider y_1, the percentage of smolts returning as adults. Table 1 shows that the April release resulted in returns of 3.13–11.58%, the May release gave increased returns of 12.39–19.02%, and the June release led to still greater returns of 24.74–43.34%. Finally, the July release gave reduced returns in the range of 4.82–20.17%. Obviously, release time affects adult returns and an analysis of the variance of y_1, in relation to the four release dates (analysis not given here), would easily prove the point.

Although the experiment was designed with analysis of variance in mind, conventional ANOVA is insufficient to capture the structure that the data suggest. Not only do differences in time of juvenile release appear to affect the outcome, they also appear to have a *systematic* effect. As the release data is delayed into June, the results increase steadily; yet further delay into July appears detrimental. Similarly, although perhaps less clearly, there appears to be a size effect. In June, for example, the juveniles most productive of adults come from the middle of the size range, whereas both smaller and larger juveniles give somewhat smaller returns.

The standard method for modeling such consistent effects of the control variables x_1 and x_2 on a response y is to fit a suitable response function to the data

$$(1)\quad y = f(x_1, x_2).$$

In the present context, an increase in x_1 or x_2 typically is beneficial to the response at first, but eventually further increase becomes detrimental. The modified quadratic surface

$$(2)\quad y = b_0 + b_1 x_1^{\alpha_1} + b_2 x_2^{\alpha_2} + b_{11} x_1^{2\alpha_1} + b_{12} x_1^{\alpha_1} x_2^{\alpha_2} + b_{22} x_2^{2\alpha_2}$$

can exhibit just such behavior, so it is reasonable to choose model (2) as a model for the data at hand. There is extensive literature on this particular function (reviewed in Lindsey et al. 1970).

In practice, model (2) commonly is viewed as the final possibility in a hierarchy of models. These include, for example, the quadratic surface

$$(3)\quad y = b_0 + b_1 x_1 + b_2 x_2 + b_{11} x_1^2 + b_{12} x_1 x_2 + b_{22} x_2^2$$

with $\alpha_1 = \alpha_2 = 1$, and the constant surface

$$(4)\quad y = b_0.$$

where all b's except b_0 are equal to zero. An analysis of variance (given later) can be used to determine which of the models within the hierarchy should be adopted. Because the final model (4) is independent of x_1 and x_2, it can be taken as a null hypothesis to be rejected if, in fact, the control variables influence the response y.

To estimate the parameters in models (2), (3), or (4) and to complete the variance analysis just described, it is necessary to introduce an assumption on the nature of statistical error in the response. The most common assumption is that errors enter additively, so that model (2) is replaced by

$$(5)\quad y_i = b_0 + b_1 x_{1i}^{\alpha_1} + b_2 x_{2i}^{\alpha_2} + b_{11} x_{1i}^{2\alpha_1} + b_{12} x_{1i}^{\alpha_1} x_{2i}^{\alpha_2} + b_{22} x_{2i}^{2\alpha_2} + \epsilon_i$$

where i (from 1 to 57) indexes the observations and ϵ_i is the random deviation of the response from the model. (The index j from 1 to 9, corresponding to different responses, is sup-

TABLE 4. Responses investigated, and their notations ($y_1, \ldots, y_9$), in relation to the control variables of time (x_1, Julian days) and size (x_2, g) at juvenile release. Table numbers in the third column refer to the tables in which the original data are tabulated.

Notation	Response	Table
y_1	Adult returns (%)	1
y_2	Jack returns (%)	1
y_3	Total returns (adults and jacks) (%)	1
y_4	Adult biomass (lb/100 000 juveniles)	2
y_5	Jack returns (lb/100 000 juveniles)	2
y_6	Total biomass (adults and jacks) (lb/100 000 juveniles)	2
y_7	Benefit−cost ratio, adult returns	3
y_8	Benefit−cost ratio, jack returns	3
y_9	Benefit−cost ratio, total (adult and jack) returns	3

pressed here.) The ϵ's are assumed to be independently normally distributed with mean 0 and standard deviation σ. This error model at best is only approximately correct for the present data. For example, Table 1 shows instances in which y_2 (% returning jacks) is 0%. If the errors were truly additive, then y_2 with finite probability could take negative values, but such values are impossible. Because of this problem, model (5) should be regarded as an appropriate description of error structure only where the response is significantly different from zero. For the practitioner this is not a troublesome restriction, as only significantly nonzero responses are of real interest.

The maximum likelihood criterion applied to model (5) leads to a least squares regression to estimate the eight unknown parameters b_0, b_1, b_2, b_{11}, b_{12}, b_{22}, α_1, and α_2. This regression is linear for the first six parameters, but nonlinear in the exponents α_1 and α_2. Appendix A describes the method used for solving the nonlinear regression problem whereby estimates are obtained for all eight parameters. There, problems with nonunique solutions are also discussed, and an estimate is provided for σ, the standard deviation of responses from the model.

Surface Optima

Once a response function is found that fits the data, it can be used to assess the nature of the system's response to control. In the present context, a key feature is the locus at which a maximum response y is achieved. At such a point the slope is zero; that is, the two equations.

$$(6)\quad \frac{\partial y}{\partial x_1} = 0, \frac{\partial y}{\partial x_2} = 0$$

are satisfied. The criteria (6) characterize not only maxima, but also minima and saddle points of the surface. The latter, saddle point or minimax, is a stationary point lying on a col between ascending ridges and descending valleys of a surface. The response function (4) almost always has a critical point (x_{1s}, x_{2s}) where (6) is satisfied. Its coordinates can be determined by the formulas

$$(7)\quad \begin{aligned} x_{1s}{}^{\alpha_1} &= (b_2b_{12} - 2b_1b_{22})/c, \\ x_{2s}{}^{\alpha_2} &= (b_1b_{12} - 2b_2b_{11})/c, \end{aligned}$$

where

$$c = 4b_{11}b_{22} - b^2{}_{12}.$$

This point corresponds to a maximum if $c > 0$ and $b_{11} < 0$, a minimum if $c > 0$ and $b_{11} > 0$, and a saddle point if $c < 0$. Proofs for these relations are given in Appendix B.

Theoretically it is possible that $c = 0$, whence formulas (7) are undefined. In practice this does not happen because c is a statistic (computed from estimates for b_{11}, b_{12}, and b_{22}), which takes the precise value 0 with probability 0. More realistically c may be small and, as a result, the estimates for x_{1s} and x_{2s} are large and outside the range of the observed data. The correct interpretation for this outcome is simply that the data indicate a trend in response but do not suggest that a critical point will be found within the observed range. A related difficulty is that the right-hand sides of (7) may be negative. In that instance we adopt the convention, used throughout, that "x^{α}" simply means "x^{α}" when $x > 0$, but "$-|x|^{\alpha}$" when $x < 0$.[2] This allows (7) to have negative solutions for x_{1s} or x_{2s}. Again, the correct interpretation is that the data indicate trends with no critical point located within the observed range.

Joint Optimality

In this paper we are concerned with nine possible responses y. The critical points (7) in fact are different for each response. It happens, for example, that the optimum conditions of time and size at release for adult survival are not the same as those maximizing the benefit−cost ratio. In such instances, sometimes it is appropriate to consider points of joint optimality for two objective functions y_a and y_b. Any such point (x_1, x_2) is determined by maximizing (or minimizing) y_b on a fixed (suboptimal) contour for y_a. In other words the joint optimality point (x_1, x_2) makes the response y_b as high as possible for a given suboptimal locus associated with y_a. We call the collection of all such points a *path of joint optimality*

[2] However the expression $x^{2\alpha}$ in (2) is interpreted as $(x^{\alpha})\cdot(x^{\alpha})$, and therefore it is always positive. This interpretation comes from viewing (2) as a variation of (3) in which x_1 and x_2 have been transformed exponentially, utilizing the convention given. Hence the convention, standard when α is an odd integer but not otherwise, extends the response function (2) to unrealistic values $x_1 < 0$ and $x_2 < 0$ in such a way that (i) the function (2) is consistent with (1), and (ii) the equations (7) always have real solutions (x_{1s}, x_{2s}) consistent with global trends in the function (2).

TABLE 5. Least squares estimates for the power parameters (α_1, α_2) and coefficients ($b_0, \ldots, b_{22}$) of the second-order polynomial (text equation 5) used to model nine responses (y_1 to y_9) of coho salmon with respect to time (x_1) and size (x_2) at juvenile release. The estimated critical point (x_{1s}, x_{2s}) is shown for each surface, along with the estimate of critical response, y_s, at that point. Bracketed critical points lie outside the observed range of the data.

Parameter estimates	y_1, returns, adults only (%)	y_2, returns jacks only (%)	y_3, returns, all fish (%)	y_4, biomass, adults only (lb)	y_5, biomass, jacks only (lb)	y_6, biomass, all fish (lb)	y_7, benefit−cost, adults only	y_8, benefit−cost, jacks only	y_9, benefit−cost, all fish
α_1	6.6890	1	6.4175	5.5270	1	5.4981	4.9443	1	4.8655
α_2	2.7113	4.0875	3.1129	2.8412	3.4257	2.9310	0.8876	2.9875	0.8129
b_0	4.0329	−9.7089	3.5769	1.2971×10^{4}	-1.0021×10^{4}	1.2845×10^{4}	6.6998	-7.0353×10^{-1}	6.966
b_1	7.7068×10^{-14}	1.5024×10^{-1}	3.1742×10^{-13}	1.6297×10^{-7}	1.5270×10^{2}	1.8941×10^{-7}	2.7016×10^{-10}	1.0917×10^{-2}	4.0476×10^{-10}
b_2	1.0322×10^{-3}	1.9425×10^{-5}	4.5079×10^{-4}	5.6882	2.1770×10^{-1}	4.6135	-5.0750×10^{-1}	3.1404×10^{-5}	-6.3297×10^{-1}
b_{11}	-4.712×10^{-29}	-5.5988×10^{-4}	-7.9545×10^{-28}	-4.4500×10^{-20}	5.7216×10^{-1}	-5.9997×10^{-20}	-1.6592×10^{-21}	-4.1234×10^{-5}	-3.7877×10^{-21}
b_{12}	1.8568×10^{-18}	-7.3261×10^{-8}	1.5437×10^{-18}	2.6329×10^{-12}	-9.5931×10^{-4}	2.1286×10^{-12}	5.0259×10^{-12}	-1.0231×10^{-7}	9.8326×10^{-12}
b_{22}	-2.2183×10^{-7}	-1.7372×10^{-12}	-1.3883×10^{-8}	-5.6159×10^{-4}	-1.0655×10^{-7}	-3.0442×10^{-4}	-1.5611×10^{-2}	-1.9205×10^{-10}	-2.6990×10^{-2}
x_{1s}(d)	173.2	(610.2)	172.7	170.0	(260.6)	169.9	(158.4)	(46.2)	(158.1)
x_{2s}(g)	25.1	(−47.7)	27.1	25.6	(−32.5)	26.0	(−5.0)	(41.7)	(−3.2)
y_s	43.5[a]	(−34.5)[b]	46.2[a]	215.0×10^{3}[a]	(-6.637×10^{3})[b]	218.0×10^{3}[a]	(17.90)[a]	(0.64)[a]	(17.92)[a]

[a]Maximum point.
[b]Saddle point.

for y_a and y_b. Geometrically, it turns out that points on this path correspond to points where the respective contours for y_a and y_b are tangent to one another.

In practice, the path of joint optimality can be useful in resolving the conflict where the critical points (x_{1s}, x_{2s}) differ for two responses y_a and y_b. As both optima cannot be achieved simultaneously, it is reasonable to select points that optimize the trade-off between them. Given that the responses y_a and y_b are of primary importance, the control variables (x_1, x_2) should at least be restricted to the path of joint optimality between them. Where a particular point is chosen on this path, and whether it is closer to the critical point or optimum y_a or y_b, depends on a decision regarding the relative importance of y_a or y_b.

Unfortunately, points of joint optimality cannot be expressed by simple formulas similar to (7). They must be determined by a recursive nonlinear estimation process (Appendix C).

INTERPRETATION OF THE ANALYSES

Use of response surface analysis leads to two further questions: (i) interpretation of the resulting surfaces, and (ii) assessment of their credibility. The first question pertains to surface shape or topology; the second involves analysis of variance. These aspects of the analysis are considered in relation to specific problems posed by the present data.

Surface shapes — Table 5 lists the complete set of estimates computed for the parameters in model (5). Estimates of the response functions y_1 to y_9, along with the critical point for each surface obtained from (7), were calculated from the data in Tables 1−3 (for computational detail, see Appendix A). The critical points (Table 5) are of four types: (i) a maximum within the observed range of the data (y_1, y_3, y_4, y_6), (ii) a maximum below the observed range in the x_1, x_2-plane (y_7, y_9), (iii) a saddle to the lower right of the observed range (y_2, y_5), and (iv) a maximum to the upper left (y_8).

These results can be interpreted in light of the contour plots shown in Fig. 2. There, three types of surface shape may be identified: (a) a surface with a peak within the observed x_1, x_2-range (Fig. 2) (y_1, y_3, y_4, y_6); (b) a ridge ascending toward the bottom of the figure (y_7, y_9); and (c) a ridge ascending to the upper left from a flat area with response near zero at the bottom of the figure (y_2, y_5, y_8). The peaks in (a) obviously match the maxima (i) just described. Similarly the ridges (b) match (ii) in the sense that the ridges appear to rise toward theoretical maxima below the x_1, x_2-range. Finally, the ridges (c) match (iii) and (iv); the ridges appear to rise toward a theoretical maximum in the upper left or they may rise from

FIG. 2. Influence of time of release (Julian days) and mean size at release (g) of juvenile coho salmon on returns at maturity (to the fence and commercial and sport fisheries): percent return of (a) y_1, adults, (b) y_2, jacks, (c) y_3, adults plus jacks; biomass of returns in thousands of lb per 100 000 juveniles released for (d) y_4, adults, (e) y_5, jacks (f) y_6, adults plus jacks; benefit−cost ratios for returns of (g) y_7, adults, (h) y_8, jacks, (i) y_9, adults plus jacks. Contours in each panel are based on equation (5) (see text) for which estimates of the parameters are listed in Table 5. In (a) the ridge of optimum release weight refers to sizes (g) at release predicted to give maximum returns for given release times; in (a), (c), (d), and (f) maximum response on the surface (y_s) is at the critical point (x_{1s}, x_{2s}).

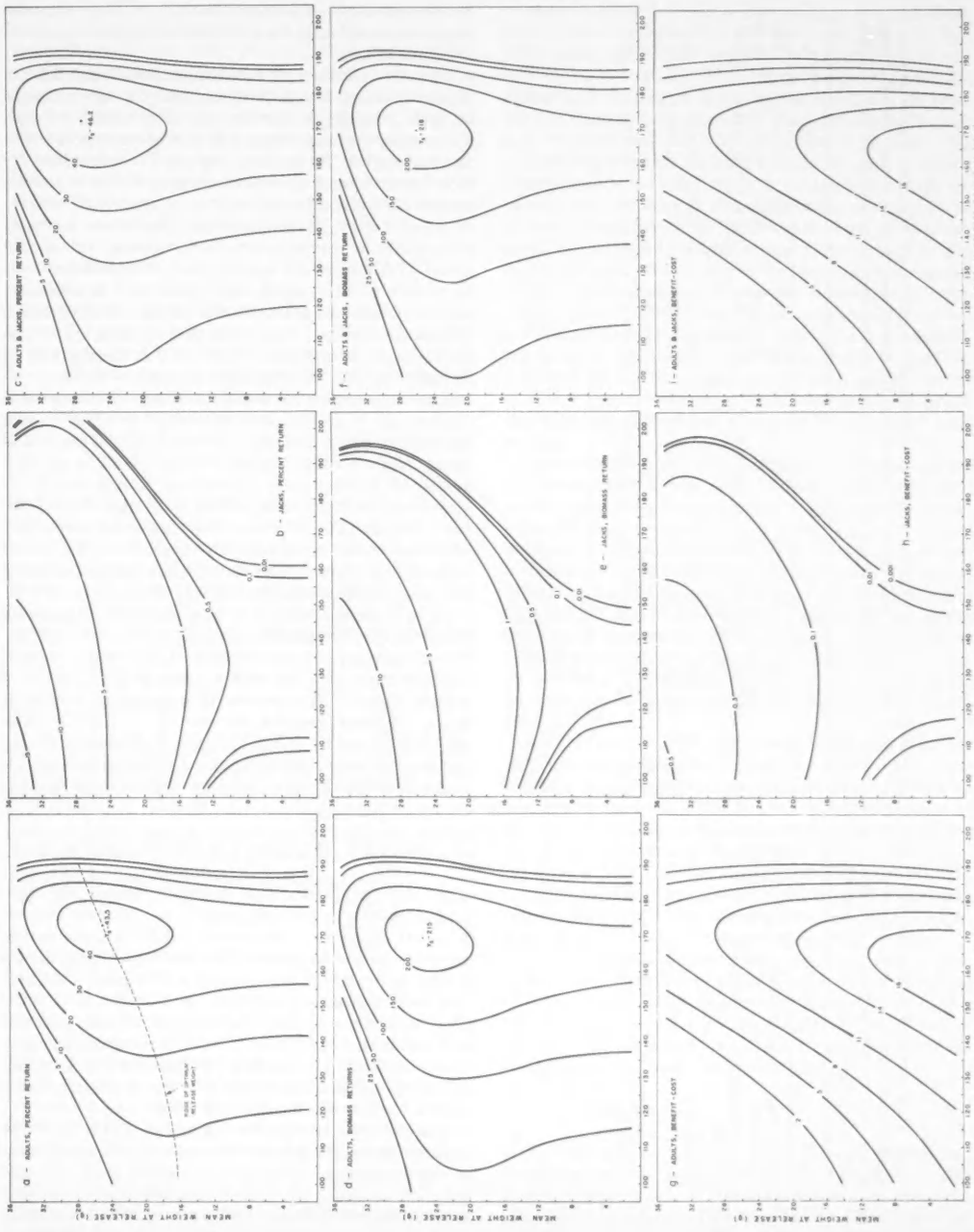
a – ADULTS, PERCENT RETURN
b – JACKS, PERCENT RETURN
c – ADULTS & JACKS, PERCENT RETURN
d – ADULTS, BIOMASS RETURNS
e – JACKS, BIOMASS RETURN
f – ADULTS & JACKS, BIOMASS RETURN
g – ADULTS, BENEFIT - COST
h – JACKS, BENEFIT - COST
i – ADULTS & JACKS, BENEFIT - COST
MEAN WEIGHT AT RELEASE (g)
TIME OF RELEASE (days from Jan 1)

TABLE 6. Unexplained variances for three models of the general form of equation (5) used to describe the responses of coho salmon to time and size at juvenile release. The first model assumes no direct time–size effect ($b_1, \ldots, b_{22} = 0$); b_0 is the mean of y for all observations. The second model assumes a time–size effect with $\alpha_1 = \alpha_2 = 1$; the third assumes an effect with α_1, α_2 as given in Table 5. Standard deviations (σ) refer to deviations between observed and predicted values. Variance refers to total sums of squares of deviations from the data points.

Model	Estimate	y_1	y_2	y_3	y_4	y_5	y_6	y_7	y_8	y_9
Only $b_0 \neq 0$;	$\hat{b}_0$ (mean)	19.20	1.26	20.46	105.8×10^3	1249	107.1×10^3	7.73	0.0690	7.80
remaining	$\hat{\sigma}$	12.36	1.72	12.96	62.2×10^3	1705	62.7×10^3	4.53	0.0792	4.53
b's set to zero	Variance	8559.2	165.69	9409.8	216.78×10^9	162.86×10^6	220.25×10^9	1151.3	0.35155	1148.4
(56 df)										
$\alpha_1 = \alpha_2 = 1$	$\hat{\sigma}$	6.95	0.70	6.95	32.5×10^3	739	32.4×10^3	2.48	0.0413	2.47
(51 df)	Variance	2461.3	24.76	2463.1	53.95×10^9	30.65×10^6	53.57×10^9	314.2	0.08681	310.8
α_1, α_2 as shown in	$\hat{\sigma}$	3.21	0.63	3.29	16.9×10^3	708	16.9×10^3	1.38	0.0394	1.38
Table 5	Variance	506.2	19.87	531.2	13.93×10^9	25.09×10^6	13.92×10^9	93.1	0.0778	93.1
(49 or 50 df)										

a saddle in the lower part of the figure. For any of these surface shapes, the data indicate either a maximum response or a trend in response within the tested x_1, x_2-range. Maxima outside the tested range have no valid interpretation except as indicators of trend.

Variance — Table 6 presents variance information that can be used to assess how well the response functions estimated in Table 5 explain the experimental observations of Tables 1–3. Three possible response models are considered. The first assumes that the observed response (57 observations for each function) bears no relation to time and size at juvenile release. Such a model would be given by equation (5) with b_1, b_2, b_{11}, b_{12}, and b_{22} all taken to be zero. In this case, b_0 simply corresponds to the mean observed response. The second model (Table 6) is the special case of (5) obtained with $\alpha_1 = \alpha_2 = 1$. This model corresponds to a response dependent on time and size at juvenile release with elliptical (or hyperbolic) contours. Finally, the third model is (5) with α_1 and α_2 values as in Table 5. This model is characterized by distorted elliptical (or hyperbolic) contours as in Fig. 2.

Each of the models has an associated number of degrees of freedom (df). In the first model there are 57 observations with one parameter (b_0) estimated, leaving 56 df. In the second model all six b's are estimated, leaving 51 df. In the third model one or both α's also are estimated, leaving 50 or 49 df. The unexplained variances in Table 5 all represent the total sum of squares (for 57 points) of deviations between observations and model predictions. The square root of the ratio of variance to df-number gives the estimated standard deviation $\hat{\sigma}$ in each case (see equation A6, Appendix A).

As an example of the use of these variances for assessing model validity, consider the percentage of juveniles that survive as adults (y_1). Mean survival is 19.20%, with a standard deviation of 12.36% and total variance of 8559.2 (units of percent squared). With model (5), assuming $\alpha_1 = \alpha_2 = 1$, the unexplained variance is reduced to 2461.2. With $\alpha_1 = 6.6890$ and $\alpha_2 = 2.7113$ (Table 5, column 2), the unexplained variance is reduced further to 506.3. The F-statistic used to reject the first model (Table 6) in favor of the final one is

$$((8559.2 - 506.2)/506.2) \times (49/(56 - 49)) = 111.4$$

with 7 and 49 df. Given these degrees of freedom, the upper limit of tabled F-values at the 5% level is 2.21; at the 1% level it is 3.01 and at the 0.1% level it is 4.24. Because the observed F-value is very much larger than any of these, there is almost no possibility that so large a difference could have occurred by chance. Intuitively, because the third model (Table 6) explains so much of the original variance with only seven additional parameters, it must be accepted. This confirms statistically not only that both time and size at juvenile release influence survival, but also that the model (5) expresses the survival response rather well.

The estimated standard deviation, $\hat{\sigma} = 3.21\%$ in this instance, suggests that points on the response surface are known to within about

$$\pm 1.96 \times 3.21\% = \pm 6.3\%$$

at the 95% confidence level. This result can be used to assess

the precision of the contours in Fig. 2 (y_1, panel 1). For example, an observed response of 30% might be expected when the predicted response lies between 23.7% and 36.3%. Hence, the contours themselves provide approximate confidence limits for each other. (This statistical approximation is valid only within the range of the observed data.) In the vicinity of the response maximum (y_s) at the critical point, only one-sided confidence limits are appropriate. Thus an observed response of 40% might be expected anywhere within the predicted 33.7% contour; consequently that contour may be used to define an approximate confidence region for the predicted maximum response on the surface. Incidentally, the highest *observed* adult survival (Table 1) is 43.34% on day 161, with a mean weight of 19.9 g at juvenile release. Predicted adult survival y_1 for these conditions is 37.37%.

In Table 6 the response functions y_3, y_4, y_6, y_7, and y_9 all lead to variance analyses similar to that described for y_1. The version of model (5) with $\alpha_1 = \alpha_2 = 1$ explains about 75% of the original variance. If α_1 and α_2 are allowed to move to their estimated values in Table 5, ~75% of the remaining variance again can be explained. The final model explains over 90% of the original variance.

By contrast, the functions y_2, y_5, and y_8, all pertaining to response of the jacks, give somewhat different results. Model (5) with $\alpha_1 = \alpha_2 = 1$ still explains over 75% of the original variance; however, the improvement possible by allowing arbitrary values of α_1 and α_2 is not so great as before. In all instances there is some advantage to be gained in allowing free values for α_2, but almost no improvement is obtained by freeing α_1. For y_2 this situation is summarized as follows:

α_1	α_2	Unexplained variance of y_2
1	1	24.76
1	4.0875	19.87
0.55293	4.2521	19.74

The third entry, although a slight improvement on the second, does not represent enough variance reduction to justify freeing the parameters α_1. For that reason, the second entry is used and not the third, as shown in Tables 5 and 6. In practice the nonlinear search algorithm employed had difficulty locating the result shown in the third entry as the sum of squares changed only slightly for rather large changes in α_1.

Results

Percent Return of Mature Fish

For adult returns (Fig. 2a), the predicted maximum return at the center of the surface (y_s) is 43.5%, corresponding to release on day 173.2 (June 22, 1975) at a mean juvenile weight of 25.1 g (Table 5). The standard deviation for percent return of adults (y_1) over the surface is ±3.21% (Table 6) and the contours are known with a precision of about ±6.3% ($P = 0.05$). The surface also shows an interaction between time of release and size at release with respect to the magnitude of adult returns. In Fig. 2a this can be illustrated as follows. A curve drawn to connect the points at which tangents to the surface contours are parallel to the axis of mean weight ($\partial y_1/\partial x_2 = 0$, equation (5)) provides estimates of release weights for which percent return of adults is maximized maximized for specified release times. Hence, from the figure, maximum returns are predicted to occur from early release of smaller juveniles and later release of larger juveniles. For the four Julian days of Table 1 (day 104, 132, 161, 189), these approximate weights are, respectively, 16−17, 18−19, 22−23, and 27−28 g. The surface also indicates that returns from releases made after approximately day 180 (June 29, 1975) can be expected to drop sharply whatever the mean size at release may be. From a practical viewpoint, a fish culturist might enquire about the width of the time "window" through which juveniles might be released with high expectation of adult returns. It is assumed that one would wish to avoid the portion of the surface to the right of y_s, where predicted returns drop sharply at later release dates. One also might define the 40% contour as the boundary for acceptable returns. Recognizing that this contour is known with a precision of about ±6.3%, one might find in some trials aimed at a 40% return that the actual returns would be as low as 34%. Interpolating, this contour could be associated with a release time at about day 163. Hence, one would conclude that fish of 22−25 g mean weight could be released between days 163 and 173 with expectations of high (40% or greater) adult returns.

For returns of jacks (Fig. 2b), predicted values on the surface increase from low mean weights over a broad range of release times toward higher mean weights at early release dates. The ridge associated with this trend ($\partial y_2/\partial x_1 = 0$) is of particular interest; it implies that *greater returns of jacks may be expected from early release of larger juveniles*. Overlaying the surface for jack returns (Fig. 2b) on that for adult returns (Fig. 2a) indicates that jack returns of about 1−5% would be expected in association with maximum and near-maximum (40% or greater) returns of adults. The standard deviation over the surface for jack returns is about ±0.63% (Table 6). Hence the contours are known with a precision of about ±1.2% ($P = 0.05$).

For the return of all fish, adults and jacks combined (Fig. 2c), the predicted maximum return at the center of the response surface (y_s) is 46.2%, corresponding to release on day 172.7 (June 22, 1975) at a mean juvenile weight of 27.1 g. The standard deviation for percent return of all fish (y_3) over the surface is ±3.3% (Table 6). Hence, the contours are known with a precision of about ±6.5% ($P = 0.05$). Comparison of the surface for percent return of all fish with that for adults only shows them to be very similar in shape. The predicted maximum response in both instances is achieved on about the same date of juvenile release, but expected maximum returns of all fish are realized from release of juveniles of a slightly larger predicted mean size of 27.1 g (Table 5). For returns of all fish there also is an interaction between time and size at juvenile release similar to that seen on the surface for adult returns (Fig. 2a).

Biomass of Returns

For returns in terms of adult biomass (Fig. 2d) the predicted maximum response at the center of the surface (y_s) is 215 thousand lb per release of 100 000 juveniles. The center (y_s) corresponds to release of juveniles on day 170.0 (June 19, 1975) at a mean weight of 25.6 g. The standard deviation of adult biomass (y_4) over the surface is ±16.9 thousand lb

(Table 6), and the surface contours are known with a precision of about ±33.1 thousand lb ($P = 0.05$). The shape of the surface and the interaction between time of release and mean juvenile weight at release again are similar to those for y_1 and y_3 (Fig. 2a, 2c). The shape of the surface for y_4 indicates that maximum adult biomass is expected from early release of smaller juveniles and later release of larger juveniles, the interaction involved being similar to that for percent return of adults.

For biomass of returning jacks (Fig. 2e), predicted values on the surface increase from low mean release weights over a range of release times toward higher mean weights at early release dates. The shape of the surface and the interaction between release times and mean release weights are similar to those for percent return of jacks (Fig. 2b). Hence the conditions at release associated with higher percent return of jacks are those leading to greater biomass of returning jacks, as might be expected. The standard deviation over the surface for biomass of jack returns is about ±708 lb (Table 6). Hence the contours are known with a precision of about ±1.39 thousand lb ($P = 0.05$).

For the biomass of returns of all fish, combining adults and jacks (Fig. 2f), the predicted maximum (y_s) at the center of the response surface is 218 thousand lb per 100 000 juveniles released. The surface center corresponds to a release of juveniles on day 169.9 (June 19, 1975) at a mean weight of 26.0 g. The standard deviation for total biomass of returns (adults plus jacks) (y_6) over the surface is ±16.9 thousand lb (Table 6); the surface contours are known with a precision of about ±33.1 thousand lb ($P = 0.05$). Predicted maximum biomass of all fish is very similar to that for adult biomass, and is achieved on the same date of release of juveniles of approximately the same size.

Benefit–Cost Ratios

The benefit–cost surfaces, relating production costs to the value of returning biomass for given times and mean sizes at juvenile release, are similar for adults (y_7) and for adults and jacks combined (y_9) (Fig. 2g, 2i). In both figures there is a rising ridge showing a trend toward increasing benefit–cost ratios extending from later release of larger juveniles toward earlier release of smaller fish. In both instances the presumed maximum response on the surface lies outside the range of the data at negative release weights near day 158 (Table 5). Obviously the estimates of the surface centers are extrapolated values and should be viewed only as indicative of trends. A biological interpretation of the location of the surface centers would suggest that maximum benefit–cost ratios might be obtained from release of small (<12 g) fish near day 160, as the mean size of the smallest release groups on day 161 (Table 1) was 12.3 g.

For benefit–cost ratios for jacks (Fig. 2h), predicted values on the surface increase from low mean release weights over a range of release times toward higher mean weights at early release dates. The presumed surface center (Table 5) is located beyond the range of the data in the direction of the rising ridge. Again, the surface center has no exact biological meaning. It may be interpreted as an estimate of the limit of the ridge describing the interaction between time and size at juvenile release. More significantly, the ridge indicates that maximum benefit–cost ratios for jacks may be expected from early releases of large juveniles. Noted also is the fact that the benefit–cost ratios for jacks (Fig. 2h) are substantially smaller than those for adults (Fig. 2g). Hence in practice one would opt to maximize benefit–cost ratios for adult returns while *minimizing* those for jacks. From the surfaces (Fig. 2g, 2h) both results would be achieved through later release of smaller juveniles.

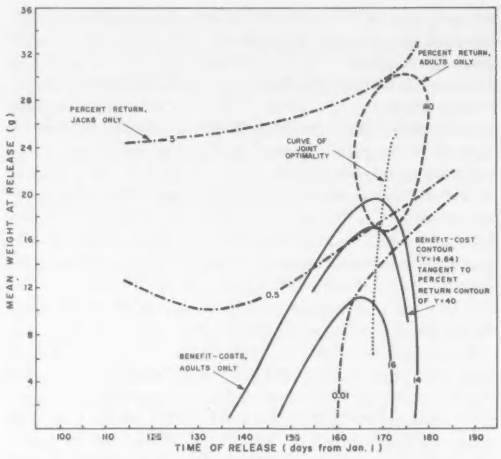

FIG. 3. Composite of portions of three of the response surfaces examined (Fig. 2) showing interrelations between percent return of adults (y_1), of jacks (y_2), and benefit–cost ratios associated with percent return of adults (y_7). The path of joint optimality runs from the center of the surface for y_1 toward the center for y_2 (located outside the factor space examined). On the path, benefit–cost ratios decrease with increasing returns of adults and jacks. Maximum adult returns are associated with less than maximum benefit–costs; conversely, higher benefit–cost ratios are associated with less than maximum adult returns. On the path, these relations between adult returns and associated benefit–costs are seen to be more sensitive to differences in mean release weights than release times.

Joint Optimality

An overlay of contours for three responses evaluated from the data is shown in Fig. 3. A central contour (40%) of the surface for percent return of adults (y_1; Fig. 2a) is shown in the upper right of the figure. Several contours (0.01, 0.5, 5%) of the response surface for percent return of jacks (y_2; Fig. 2b) also are shown. In addition, several contours (14, 14.64, 16) of the benefit–cost ratio surface for adult returns (y_7; Fig. 2g) are shown in the lower right. Also shown is the path of joint optimality running from the center of the surface (y_s) for percent return of adults (y_1) toward the center of the surface for benefit–cost based on percent return of adults (y_7). The center of the latter surface is outside the release time–release weight factor space considered; hence, benefit–cost estimates at low mean release weights (e.g. <6 g) presumably have doubtful value.

The composite of surface contours (Fig. 3) indicates, in general, that maximum and near-maximum predicted return

TABLE 7. Selected points on the path of joint optimality between the center of the surface for percent return of adult coho, and that for benefit−costs associated with adult returns. Each locus is defined in terms of a time of release and mean weight at release at which the adult returns and benefit−costs are jointly determined.

Coordinates of surface		Response	
Release time (d)	Mean weight (g)	Adult returns (%)	Benefit−costs ($/$)
173.1[a]	25.1[a]	43.5	12.2
172.9	24.7	43.5	12.4
172.3	24.0	43.4	12.6
171.7	23.0	43.1	13.0
171.0	21.1	42.4	13.5
169.6	16.9	40.0	14.6
169.1	15.2	39.0	15.1
168.7	13.3	38.0	15.5
168.3	11.0	37.0	16.0
168.0	7.5	36.0	16.5

[a]Locus of center of surface for percentage adult returns.

of adults is associated with percent returns of jacks ranging from about 0.5 to 5%. Furthermore, maximum and near-maximum adult returns are obtained at less than maximum benefit−costs. As one moves upward toward higher mean release weights on the path of joint optimality, adult and jack returns increase and benefit−cost ratios decrease. With movement upward on the path of joint optimality the time to release, for maximum adult returns, increases slightly. By comparison, however, the relation between adult returns and benefit−costs related to adult returns is more sensitive to differences in mean release weight than time of release. The relations between release time, mean weight at release, adult returns, and associated benefit−cost ratios are shown for selected points on the path of joint optimality in Table 7. The following observations are summarized from the table. (1) At the center of the surface for adult returns (y_{1s}, 43.5%) a benefit−cost ratio of 12.2:1 is predicted. (2) The optimum time of release of juveniles is relatively constant (days 168.0−173.1) on the path of joint optimality. (3) Release of smaller juveniles on or near day 170 should increase monetary benefits relative to production costs, while at the same time maximizing yield of adults with respect to suboptimum mean release weight of juveniles. (4) Conversely, higher adult returns are coupled with increased returns of jacks, presumably a major reason for the concomitant reduction in benefit−costs in moving on the path of joint optimality toward the center of the surface for adult returns.

Discussion

ASSESSMENT OF EXPERIMENTAL DATA

One important potential source of error, among those that could influence the results, lies in the uncertainty of recovery of tagged individuals caught by the commercial and sport fisheries. As mentioned previously, the proportion of juveniles from each release group recovered in the commercial fishery as adults was estimated by sampling the commercial catch at an intensity of 20%. Size selectivity of commercial gear against capture of jacks resulted in the likelihood that virtually all of the jacks were recovered at the hatchery fence. In addition, estimates of the number of fish in each release group captured by the sport fishery were based on the recognition and reporting of marked fish. The awareness factor (0.28), used to adjust for the incomplete recognition of marked fish in the sport fishery, itself is subject to considerable uncertainty. Only counts of fish returning to the hatchery weir can be considered to be without error; all fish returning to the weir were a product of the experiment and all were sampled.

A further potential source of error arose from the fact that all of the original experimental fish in each pond were graded into three size groups (small, medium, large) prior to tagging. It could be argued that this method of setting up size groups to determine the influence of juvenile size on success of return might be biased, for the following reasons. There is accumulating evidence (Ricker 1972) suggesting that hereditary factors are at least partly involved in rate of growth and age of return at maturity. Although the available evidence as yet is not at all clear, it appears that predisposition toward early maturity may be genetically induced, finding its full expression when favorable environmenal circumstances, such as abundant food supply, favor rapid growth. If this proposition were true, then some proportion of the faster growing, larger male juveniles in a population would show a greater propensity to mature earlier and return as jacks. Hence, it could be argued that selection of "large" juveniles in the current study would result in an inflated proportion of jacks originating from the "large" juveniles, a proportion that more properly should apply to the population as a whole from which the "small, medium, and large" groups were drawn. In view of this potential difficulty, there is an alternative to grading a population into size groups, i.e., to grow three populations, in this instance, at different rates (temperatures) and to divide the three populations among the various release times. Yet theoretically even this alternative might bias the results. It is possible that growth at different temperatures may lead to differences in biochemical composition or fish "quality," which itself may influence survival potential. In addition, although temperature manipulation of growth rate seems a very plausible alternative, it often may be difficult to put into practice. Most hatcheries do not have the temperature control and space required for growing a substantial array of fish groups under experimental conditions.

The question of grading fish into size groups subsequently led to further inspection and analysis of the original data (Bilton 1978). These data indicate that the proportions of jacks returning from the graded groups released in April, May, and June were not demonstrably different, for a given size, than the proportion returning to a combined population of small, medium, and large release groups having the same mean size. There was one exception among the groups compared: a higher proportion of jacks than expected returned from the June release of large juveniles. In the language of analysis of variance there are two sources of variance that refer to size effects: the mean weight in grams of juveniles in a release group, and the designation of the group size (small, medium, large) at release. With the exception of the June release of large fish just noted, analysis of variance showed that information on groups did not add significantly to that provided by mean release weight in explaining jack returns.

On this basis we assume a small bias occurs in relation to the June release of large juveniles; however, we also presume this bias would have only a minor influence on the production equation relative to the total variance associated with treatment effects. Hence, returns of jacks can be explained on the basis of mean release weight, and designated release groups did not add significantly to the explanation of variance. For the adults a similar analysis showed that the extra information provided by grouping did not explain any significant portion of the variance associated with adult returns. Hence, for both jacks and adults, there was little evidence to support the possibility that genetic factors influenced the returns through the grading technique used. Yet, the evidence from other sources suggests that hereditary factors are at least partly involved in expression of growth rate and age of return. Therefore the inference that genetic factors could influence adult and jack returns would appear to remain valid. We conclude that grading could produce minor alterations in the curvature of a response surface for adult or jack returns, while not altering the general configuration of the surface itself. Given these uncertainties we conclude that different size groups should be obtained, where possible, through temperature-controlled growth rate rather than grading of populations into size groups.

In the current study, marking and nose tagging of all fish groups occurred several weeks prior to each release (Bilton and Jenkinson 1976). The period between tagging and release, used to evaluate tagging mortality and tag retention, was short. In some instances in similar studies it may not be possible to mark and tag the fish close to the time of release. In some hatchery situations, if water temperatures are higher than desirable, the stress imposed from crowding and handling during marking and tagging may trigger outbreaks of disease. To avoid such problems may require that grading and tagging occur several months (even the previous fall) prior to release, when water temperatures are lower. In the ensuing interval between tagging and release, significant growth may occur. Also, with a more prolonged period between tagging and release, an exact inventory of numbers released may be more difficult to obtain. Under such circumstances, sampling the groups for estimates of mean size and sex ratio just prior to release is of paramount importance.

In addition to the factors outlined that could influence the design and interpretation of the experimental results are those that would apply on a larger scale at various production hatcheries. There are two general variables that could influence the interpretation of the effects of time and size at release on the success of returns of mature fish. These are the influences of (1) site-specific variation and (2) annual variation on the biological system examined. A number of site-specific factors unique to the Rosewall Creek experiment could have influenced the release–return relations obtained. These could include the diet provided the cultured fish, the feeding rate, the temperature regime, the characteristics of the water supply, the genetic nature of the fish stock used, rearing density and associated water quality, diseases endemic to the water system used in culture, and the type of estuary that the fish would enter upon release. In effect, the background variables of the experimental system, their levels, and combined effects might produce different release–return relations if the current experiment were to be repeated at other sites. Therefore general application of the results for coho from the present experiment could be modified by site-specific factors, which together could form sets of unique background conditions in similar studies repeated elsewhere. The situation might be stated as follows. A specific hatchery may require "tuning" to optimize time and size at release, where the processes involved are influenced by an unrecognized and uncontrolled set of background variables associated with a given culture site.

The second source of variability is that associated with annual variation in factors influencing survival of juveniles following release. Juvenile coho emigrating into the nearshore and coastal ecosystem, and their growth and survival therein, may be influenced by annual variations in meteorological and oceanographic events that in turn could affect the food web in which the juveniles act both as foragers and as prey for other species. Thus annual variability in the timing and magnitude of cyclic events in the nearshore and coastal ecosystem could act as a further source of error in the prediction of optimum conditions of time and size at release, not only for cultured fish but also for wild progeny subjected to the same postmigration conditions. In general, further examination of the influence of time and size at release of juveniles on returns of mature fish would seem to require recognition of sources of variation within and between sites and between different brood years.

Comparison of Experimental and Production Hatchery Returns

Some appreciation of the potential variability in returns, associated with different sites and brood years, may be obtained from an overlay of the response surface generated from the Rosewall Creek experiment in relation to 1971–74 production hatchery returns in British Columbia (E. A. Perry, Vancouver, B.C., personal communication) (Fig. 4), and to Washington State (USA) (R.C. Hager, Olympia, WA, personal communication) hatchery returns for the 1971–73 brood years (Fig. 5). The British Columbia production hatchery data conform in general with the predicted surface for percent adult returns generated from the Rosewall Creek data, assuming that the surface contours describing the latter are known with a precision of ±6.3%. However, the data are insufficient to indicate whether the differences between the returns to the three British Columbia production hatcheries and the Rosewall Creek site (Fig. 4) could be ascribed to site-specific or annual differences in potential for return. Of the points on the surface, six represent "accelerated" or zero-age juveniles (Bilton and Jenkinson 1980a, b) released in the year of hatching (Fig. 4; site C, 1973 brood year). Three of these, describing releases on day 162 (June 10, 1974) at average weights of 6, 8, and 14 g, are shown in the figure. Also shown are three releases of normal-age juveniles (1-yr-old, site C, 1972 brood year) released on the same day at average weights of 11, 17, and 23 g. Percentage returns from the former (0.7, 2.5, 7.4%) are considerably lower than those from the normal-age migrants (42.1, 48.3, 46.5%). The fact that both groups were released on the same day, and that the ranges of average release weights of the three releases in each of the two groups overlap, strongly suggests that factors other than time and size at release are important in deter-

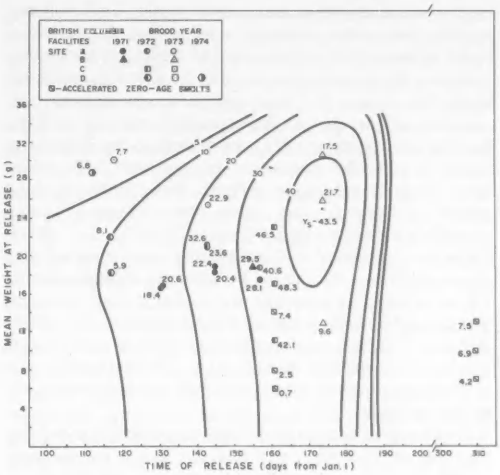

FIG. 4. Release (time, Julian days; size, mean weight, g) and return (adults, percentage) data for coho salmon from three southern British Columbia production hatcheries (sites A, B, D) overlaid on the contours for percentage adult return generated from the Rosewall Creek (site C) experimental data. Six zero-age (accelerated) releases shown are not strictly comparable with the remaining estimates (see text). Attention is drawn to the six (site C) estimates for releases on day 162; these compare returns for zero-age and normal-age migrants released at different mean weights (see text). y_s, predicted response at the surface center; contours, percent return of adults (Rosewall Creek data).

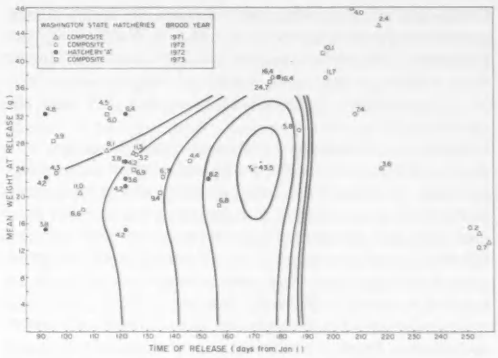

FIG. 5. Release (time, Julian days; size, mean weight, g) and return (adults, percent) data for coho salmon from representative Washington State (USA) hatcheries overlaid on the contours for percent return of adults generated from Rosewall Creek (British Columbia) data. Symbols represent data from four hatcheries; for three of these, "composite" estimates represent averaged returns for numerous release groups having identical or nearly identical release times and mean weights within the brood years indicated. y_s, predicted response at the surface center; contours, percent return of adults (Rosewall Creek data).

mining the success of return. The differences in returns cannot be attributed to different lengths of sea life prior to return; both the zero-age and 1-yr-old migrants returned as jacks and adults, respectively, in the fall of 1974 and 1975. It could be inferred that the accelerated fish may not have been physiologically ready to migrate, even when released at the same time and (by interpolation) at similar sizes. The data are minimal but suggestive that zero-age smolts, as currently produced, may prove ineffective as a means of building up stocks of coho salmon through hatchery manipulation.

The British Columbia production hatchery data (Fig. 4) portray a pattern of releases presumably influenced in the freshwater phase by site conditions as well as operator decision on the timing of release. In the figure there is a cluster of releases between days 130 and 160 approximately, and at mean release weights of 16–23 g. This cluster reflects, in part, attainable weight in relation to available growing conditions, as well as operator decision that better returns may be obtained from May to early June releases. In comparison, the Rosewall Creek data and their estimated precision suggest that high adult returns (≥40%) should be obtained from releases between days 163 and 173 at mean release weights of 22–25 g. Thus the operator appears to promote releases several weeks earlier than the Rosewall Creek data would suggest for optimizing adult returns. In addition, the production hatchery data illustrated (Fig. 4) show an average return of about 25%, whereas returns of 38–50% appear attainable based on the Rosewall Creek experiment. The potential twofold increase in returns suggested provides a target for improvement of production hatchery efficiency, achievable through optimization of time and size at juvenile release. However, confirmation of this potential will require a substantial accumulation of production hatchery data, particularly in areas of the surface for time and size at juvenile release that remain inadequately or only modestly sampled.

In comparison with British Columbia hatchery returns, those for the Washington State hatcheries (Fig. 5) show a rather different pattern of returns in relation to data on juvenile release. An average of the estimates of percent adult return from the figure is about 7%, between one-third and one-quarter of the average for British Columbia facilities. Ultimately it may be found that conditions of time and size at juvenile release, maximizing Washington State hatchery returns, may differ from those suggested by the British Columbia data. The assumed poor correspondence between the Rosewall Creek and Washington State results may arise through the influence of other factors as yet unrecognized. Nevertheless, the Rosewall Creek data provide the basis for a comparison that otherwise could not be made. Accepting the Rosewall Creek response surface patterns in this manner, the following observations can be made. Many of the points for Washington State hatchery releases (Fig. 5) represent returns for juveniles released early (before day 130) at a relatively large mean weight (>20 g). The Rosewall Creek contours for percent return predict poor returns associated with those release conditions. In addition, no releases appear to have been made in the region of the surface where maximum returns might be anticipated (163–173 d, 22–25 g). However, in the earlier period between days 150 and 163 there are two estimates of returns (Fig. 5) from the American hatcheries, 6.8 and 8.2%. These values are much lower than the range of Canadian hatchery returns for the same time period

(28.1–48.3%), suggesting that optimum conditions of time and size at juvenile release may differ in Washington State hatcheries. The highest returns obtained from Washington State releases in the figure appear to occur for large (e.g. 36–37 g) juveniles released between days 175 and 180 (16.4–24.7%).

In these comparisons of American and Canadian production hatchery returns it must be remembered that assumptions and conclusions are based on the available data. Areas of the time–size release surface for which there are few or no data could alter preliminary conclusions if data were available for those poorly sampled areas. Obviously, two-factor designs involving a grid of juvenile release times and sizes are required to provide, efficiently, the type of data leading to the optimization of release conditions that will maximize hatchery returns. Practically speaking, a completely orthogonal grid design, in which the small, medium, and large release sizes are identical at each release time, probably is impossible to achieve due to growth of the cultured fish between releases. However, we suspect that biases introduced through lack of design orthogonality will not interfere seriously with ultimate interpretation of the results of such tests. On the other hand, if production hatcheries were to accept the Rosewall Creek results without question and make the majority of future releases near the presumed center of the surface for adult returns, then returns could improve, yet the assumptions underlying the relations between time and size at release and adult returns could remain much at their current level of understanding. Therefore, we recommend that the Rosewall Creek model be viewed as the best current representation of the data, and that multifactor designs be employed to investigate further the influence of time and size at release on the success of adult returns.

Rationale for Optimizing Time and Size at Release

Optimum release "windows" — The nature of the surfaces relating release conditions to success of adult returns suggests that some underlying biological phenomenon must be operating on the migrating juveniles. Many factors may influence the life cycle of salmonids from seaward migrants to returning spawners, including migration to the sea, nearshore and coastal ecology, offshore migration, conditions on the high seas, returning migration at maturity, and ascent into fresh waters to spawn. We suspect that time and size at release may have a dominant influence on success of returns through conditions the juvenile migrants experience in the several months following migration to salt water. The major factors suspected to be operating on juvenile survival, as outlined earlier, are food supply and predation. For example, optimum conditions of time and size at release may be those providing for entry of juveniles into the nearshore and coastal ecosystems at a time and size when maximum advantage can be obtained from the available food supply in terms of growth rate and survival. The attainment of such an advantage may itself be dependent on the injection of juveniles into the ecosystem at a time when the presence and abundance or density of forage organisms of a particular type and size allow for maximum food intake relative to the cost of energy expended in foraging. Conditions that maximize the food supply, such as the onset of the spring plankton pulse, in turn may vary geographically and temporally in relation to meteorological and oceanographic events in the nearshore and coastal marine environments. Regional and annual variations in the timing of these events could influence the food supply and feeding opportunities, and hence the growth and survival of the new migrants in salt water. We assume that rapid growth is advantageous; susceptibility of juveniles to size-dependent predation could be foreshortened by more rapid growth through the intervals of higher vulnerability assumed to be associated with smaller size. Japanese experience suggests that release of chum salmon (*O. keta*) fry may require the avoidance of coastal migrations of predator fishes (Iioka 1976; Iioka et al. 1977). Therefore, maximized adult returns may result from injection of juveniles into the marine environment through specific release windows where time and size at release maximize feeding and growth potential through episodes of vulnerability to predation whose impact on survival declines with growth and increasing juvenile size. This hypothesis could apply to the survival potential of both hatchery stocks and natural migrants.

Exploring the biological rationale suggested as underlying the observed phenomenon of time and size at release could provide a more precise technology for hatchery operations. Examination of oceanographic and meteorological events in association with structured releases of juveniles over a period of years should provide insight into correlations between success of return of spawners and ecosystem parameters in the initial juvenile marine phase. The concept of course is related to that of the Japanese "plankton watch" of recent years. From such associations simple "flags" might be recognized, such as threshold temperatures in the nearshore environment, signaling the beginning of improved options regarding time of release. Sea surface temperature appears to be used to determine time of release in some Japanese chum salmon hatchery operations (Hokkaido Salmon Hatchery 1976; Iioka et al. 1977). It is conceivable that the hypothesis outlined regarding entry of juvenile migrants into the nearshore and coastal marine environment may apply to all of the Pacific Coast anadromous salmonids. A knowledge of correlative factors in the initial marine phase and their use as flags with respect to time and size at release could serve to "tune" hatchery sites to minimize both site-specific and annual variations in return of spawners.

Conditions influencing juvenile growth and development — The release of cultured juveniles from hatchery facilities at specific times and sizes requires a consideration of growth rates needed to achieve target sizes at time of release. Two options are presented: (1) to manipulate growth rate to utilize release windows, or (2) to locate hatchery facilities on water systems affording easy achievement of appropriate size at optimum time of release. Temperature is the dominant factor influencing growth rates, and the two options differ mainly in the amount of temperature control available to the fish culturist. In terms of temperature control the latter option would be simpler and less expensive. In "warm-water" hatcheries, where ambient temperatures over the winter period may be 8–10°C, growth would be more rapid than in "cold-water" hatcheries, averaging 2–5°C over the winter period. Recent evidence (C. Clarke, Nanaimo, B.C., personal communication; D. Higgs, Vancouver, B.C., personal communication) also indicates that the effects of dietary protein–fat ratios on

growth rates of salmonids are temperature dependent. In addition, evidence suggests that withholding of food can be deleterious to fish quality and possibly survival in warm-water hatcheries but not in cold-water hatcheries (Bilton and Robins 1971; K. Sandercock, Vancouver, B.C. personal communication). In general, control over growth may be achieved by temperature manipulation, by reduced feeding in cold-water hatcheries, or by alteration of protein–fat ratios in warm-water or cold-water culture. Pond loading or fish density also can influence growth rate. However, controlling growth through manipulation of pond loading should be regarded with caution; Sandercock and Stone (1979) have found an inverse relationship between pond loading rate in the juvenile stage and subsequent survival and return of adults.

Clarke and Blackburn (1978) have found that migration readiness can be judged in terms of clearance rates of sodium from the blood of juveniles transferred to salt water. The rate at which adjustment of sodium level occurs appears to be maximized in relation to the presumed normal migration period. Clarke and Shelbourn (1981), working with zero-age accelerated coho juveniles of Big Qualicum River origin, found that rates of sodium clearance were maximized at a temperature of 14°C near June 30. Submaximum clearance rates occurred at supra- and sub-optimal temperatures. Their data also suggest that submaximum clearance rates may remain at peak levels for shorter periods at colder (<10°C) than at warmer (>14°C) temperatures. Hence for accelerated fish, clearance rates relative to migration readiness appear to be temperature dependent. Also, the period of maximum clearance rate, relative to the size of the release window, may be shorter in colder culture waters. Similar studies would be most useful in relating sodium clearance rates to optimum conditions of time and size at release using normal-age juveniles.

Conditions influencing benefit–costs — The relations between success of adult returns and benefit–costs of hatchery production were described on the basis of simplified costs and dollar returns. The criteria for describing such relations could be modified to fit more closely the benefits and costs of production hatchery activities. In general, however, the Rosewall Creek experiment indicates that one could optimize the culture system either for maximum adult production or for maximum benefit–costs. The path of joint optimality (Fig. 3) shows that maximum or near-maximum benefit–costs are achieved from releases of smaller juveniles at the expense of some loss in potential returns of adults. Conversely, maximum adult returns are achieved through release of larger smolts at less than maximum benefit–costs. As one moves upward on the path of joint optimality, adult and jack returns increase and benefit–cost ratios diminish. In all of these options (Table 7) the calculated release times, maximizing adult returns and benefit–costs jointly, occurred within a rather narrow computed range of ~ 168–173 Julian days.

Rearing strategies and optimization — Heretofore, the problem of optimization has been approached as if the time of release (x_1) and mean weight at release (x_2) were mutually independent variables. For example, the center (x_{1s}, x_{2s}) on the surface for percent adult returns (Fig. 2a) gives conditions for optimal adult returns if indeed juvenile coho can be reared to mean weight x_{2s} at the time x_{1s}. The ridge of optimum release weight (Fig. 2a) represents a variation on this idea. If the release time (x_1) is prescribed by hatchery requirements, then the corresponding weight x_2 on this ridge is optimal for adult returns. Again, this presupposes that a particular juvenile mean weight x_2 is exactly achieved at a particular time x_1. Further, if two responses, such as percentage adult returns (Fig. 2a) and benefit–costs (Fig. 2g), are to be considered simultaneously, then the path of joint optimality represents optimal release conditions for various levels of trade-off. Once more, to achieve a specific point on this path, juvenile coho must be reared to a particular weight at a particular time.

When the question is raised as to *how* the surfaces should be "climbed" to achieve optimum conditions it is obvious that growth ($\Delta x_2/\Delta x_1$) is involved and the variables no longer can be considered independent. Growth, to achieve a target size at a given time, would be subject to constraints such as (1) initial weight, (2) conditions influencing growth rate, and (3) the range of growth rates attainable by the species in question. Temperature is a dominant factor influencing growth. Hence temperature could require the most attention, particularly in hatchery culture where temperature control, if available, might be modest at best. Recently, McLean (1979) examined a number of variables associated with growth of salmonids in culture. His generalized growth and rearing model would allow prediction of growth, in a manner similar to that of Stauffer (1973), under variable environmental conditions including temperature, aspects of water quality, ration level, water exchange rate, and fish density in culture. Given that some prior knowledge of expected ambient temperatures and possible feeding rates was available, growth rates could be backcalculated from the locus of optimum release conditions on a response surface to explore growth rates and initial weights required to achieve those conditions.

Estimates of growth that might be attained in practice are suggested in Fig. 6. There, surfaces for percent adult returns (Fig. 2a) and benefit–costs associated with adult returns (Fig. 2g) are superimposed and overlaid with three growth lines (G1, G2, G3). The lines G2 and G3 are constructed, as reasonable examples, from the data for small and large juveniles, respectively, in Table 1 (pond 1). The line G1 is hypothetical and has been added to complete the argument. Loci at which the growth lines are tangent to surface contours estimate release conditions that maximize response for juveniles growing at the rates indicated. These loci are shown for the benefit–cost and percent adult return surfaces, respectively, by points *a* and *b* in the figure. For each growth line it is seen that size attained, relative to attendant growth circumstances, forces a decision governing release time at which either benefit–costs or percent adult returns would be maximized. For maximum benefit–costs these release times occur between days 163 and 168 (tangents *a*); maximum percent adult returns occur later between days 171 and 173 (tangents *b*).

The growth line examples in Fig. 6 are indicative of the importance of culture temperature and feeding rate and their potential for manipulation in attempts to optimize time and size at release. The benefits of optimizing release conditions suggest the need for substantial exploration of growth control as a means of achieving that objective. Such trials presumably would consider restricted feeding or withdrawal of food during the winter period of low ambient water temperatures, and growth potential at higher temperatures in relation to feeding

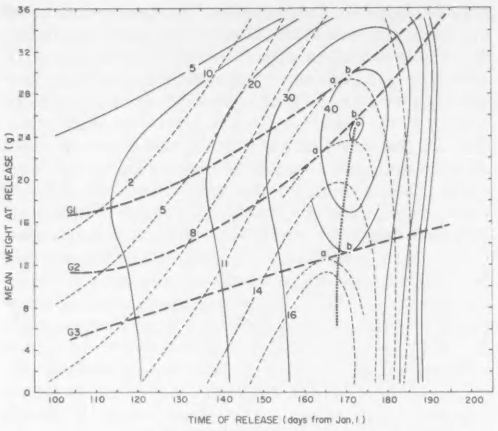

FIG. 6. Potential for optimization of release conditions for coho juveniles cultured under sets of suggested environmental constraints. Two surfaces are superimposed, that for percent adult returns (solid contours 5, 10, 20, 30, 40%) and that for benefit−costs associated with these returns (broken contour lines 2, 5, 8, 11, 14, 16). The path of joint optimality also is shown. Potential growth lines (G1, G2, G3) illustrate how the surfaces may be "climbed" under the constraints of possible conditions influencing growth; these are tangent to contours of the benefit−cost surface at points *a*, and to contours of the percent adult return surface at points *b*. Rapid growth (G1) or slow growth (G3) could prevent the attainment of ultimate optimum release conditions for adult returns, which are nearly reached on line G2 at *b*.

rates and food conversion efficiency. Information on growth potential and growth control should provide further insight into the relative effectiveness of ambient temperature regimes (cold-water vs. warm-water conditions) at various hatchery sites, and the possible advantages of temperature control. For example, if growth line G3 were representative of a cold-water hatchery, that system would be unable to reach its full biological potential for culture of coho with respect to adult returns. If the G1 line were representative of a warm-water hatchery, optimum release conditions for coho might not be attainable because of too rapid growth. In contrast, the line G2 represents the situation where near-optimum conditions of time and size at release are achieved, leading to near-maximum adult returns. It is possible that further knowledge of growth potential and growth control for a given species also might assist in determining the optimal use and placement of new hatcheries relative to the constraints imposed by ambient temperature regimes or the need for temperature control.

Rearing other salmonid species — We assume that response surfaces analogous to those for coho salmon juveniles will be found to apply in other species of Pacific salmon and steelhead (*Salmo gairdneri*) in their North Pacific Ocean range. Until more evidence is available, it is presumed that response surfaces based on time and size at juvenile release may be fairly specific with reference to (1) genetic differences between stocks, (2) local geographic, climatic, and ecological conditions, (3) gross geographic, climatic, and ecological differences (e.g. Alaska vs. California), (4) differences between species, including those associated with variation in freshwater residence and years of marine life before maturity, and (5) annual differences in climatic and oceanographic events.

Response surface configuration in the chum (*O. keta*) and pink (*O. gorbuscha*) salmon may differ from that of the coho, as both species migrate to sea as fry. The response surfaces for chum and pink salmon also may vary because of differences between them in years of sea life prior to maturation. Benefit−cost surfaces of seagoing chum and pink fry should differ markedly from those of coho, chinook (*O. tshawytscha*), and steelhead; perhaps they would show major benefits from warm-water incubation and rearing, with release occurring at the appropriate time but at a larger size. Examination of the relations between time and size at release that maximize returns and benefit−cost ratios in hatchery production of chinook salmon and steelhead should be instructive; populations of both salmonids currently show substantial decreases compared with historical levels, and both are subject to increasing artifical culture in British Columbia waters.

For the coho salmon, influence of time and size at release, and their effects on adult returns, are seen as inputs and outputs of an ecological system whose central components are not yet well understood. We suspect that nearshore and coastal ecological dynamics may be particularly involved. Events in early marine life of salmonids are likely to have a major impact on the survival potential of individuals and stocks in a manner similar to that of the "critical theory" of survival of year classes of marine fishes (May 1974). As food preference varies among the species, the ecological dynamics associated with food supply, growth, and survival in nearshore and coastal waters may vary accordingly. We suspect that investigation of the ecological dynamics of entry, feeding, and growth of juvenile salmonid populations in such waters would provide a better understanding of the biological nature of the time and size at release phenomenon, leading not only to improved hachery production strategies but also to improved management of natural populations. Toward this goal, the Rosewall Creek data show that the returns of hatchery-produced coho adults may be raised from a current average of 25% to a maximum near 50% in southern British Columbia waters. In addition, site-specific and annual variability in returns of hatchery-produced coho salmon currently are being investigated through the release of similar arrays of juvenile groups at two southern British Columbia hatcheries.

Acknowledgments

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Appendix A. Estimating Parameters in (5)

Define the two parameter vectors

$$\theta_1 = (b_0, b_1, b_2, b_{11}, b_{12}, b_{22}),$$
$$\theta_2 = (\alpha_1, \alpha_2).$$

The problem is to find estimates $\hat{\theta}_1$ and $\hat{\theta}_2$ that minimize the sum of squares

$$\text{(A1)} \qquad S(\theta_1, \theta_2) = \sum_{i=1}^{n} [y_i - b_0 - b_1 x_{1i}^{\alpha_2} - b_2 x_{2i}^{\alpha_2} - b_{11} x_{1i}^{2\alpha_1} - b_{12} x_{1i}^{\alpha_1} x_{2i}^{\alpha_2} - b_{22} x_{2i}^{2\alpha_2}]^2,$$

given the observations (x_{1i}, x_{2i}, y_i), $i = 1, \ldots, n$ (where $n = 57$ here), that is, to find $\hat{\theta}_1$, $\hat{\theta}_2$ so that

$$\text{(A2)} \quad S(\hat{\theta}_1, \hat{\theta}_2) = \min_{\theta_1, \theta_2} S(\theta_1, \theta_2).$$

As a first step, notice that for a prescribed parameter vector θ_2 (i.e. prescribed α's) the quantity

$$\text{(A3)} \quad S_1(\theta_2) = \min_{\theta_1} S(\theta_1, \theta_2)$$

can be found explicitly. This can be done by regarding the minimization problem as a six-variable *linear* regression for θ_1 from the data $(x_{1i}^{\alpha_1}, x_{2i}^{\alpha_2}, y_i)$, $i = 1, \ldots, n$.

In this way, estimates $\tilde{\theta}_1(\theta_2)$, which depend on the given value of θ_2, are obtained. These estimates solve the least-squares problem (A3), that is,

$$\text{(A4)} \quad S_1(\theta_2) = S(\tilde{\theta}_1[\theta_2], \theta_2).$$

The function $S_1(\theta_2)$ is a well-defined, though complicated, function of the two variables α_1 and α_2. The problem of minimizing S in (A1), a function of eight variables, is thus

reduced to the more manageable problem of minimizing S_1 in (A4), a function of two variables. In other words if $\hat{\theta}_2$ minimizes S_1, then it also minimizes S with

$$\hat{\theta}_1 = \tilde{\theta}_1(\hat{\theta}_2).$$

With these ideas in mind, a computer was used to solve the problem (A2). It employed the simplex method of searching for a function minimum, as conceived by Nelder and Mead (1965) and implemented by O'Neill (1971). This method works quite well with only two variables, and it was applied to the function S_1, given by (A4). Notice that the actual calculation of $S_1(\theta_2)$ involves first performing the six-variable linear regression (A3).

Interestingly, the problem (A1) may not have a unique solution. Sometimes there are four local minima for S in which the signs of (α_1, α_2) are, respectively, $(+, +)$, $(+, -)$, $(-, +)$, and $(-, -)$. This fact is not too surprising when one realizes that the values $\alpha_1 = 0$, or $\alpha_2 = 0$ are singularities. For example, if $\alpha_1 = 0$, then the response function (4) no longer depends on x_1. One can reasonably take the point of view that four distinct models are available corresponding to the four choices of sign for (α_1, α_2). In this paper, the model with both α's positive was always selected. Other possibilities (including the log transformation as a counterpart to the possibilities $\alpha_1 = 0$ or $\alpha_2 = 0$) did not give better results.

Once $(\hat{\theta}_1, \hat{\theta}_2)$ is found, the maximum likelihood estimate for the variance σ^2 turns out to be

$$\text{(A5)} \quad \hat{\sigma}^2 = \frac{1}{n} S(\hat{\theta}_1, \hat{\theta}_2).$$

This is known to be biased (especially for small n), and a preferred estimator is

$$\text{(A6)} \quad \sigma^2 = \frac{1}{n-k} S(\hat{\theta}_1, \hat{\theta}_2),$$

where k is the number of parameters estimated. Here $k = 8$ ordinarily, but k might be 7 or 6 if α_1, α_2, or both are fixed at 1. The usual argument in going from (A5) to (A6) depends on linear approximations when some parameters, such as α_1 and α_2, enter nonlinearly. All estimates cited in this paper were obtained from (A6).

Appendix B. Technicalities of Locating Optima

For the particular response function (4), the equations (6) become

$$\text{(B1)} \quad \begin{aligned} b_1 + 2b_{11}{x_{1s}}^2 + b_{12}{x_{2s}}^2 &= 0, \\ b_2 + b_{12}{x_{1s}}^2 + 2b_{22}{x_{2s}}^2 &= 0. \end{aligned}$$

These are a pair of linear equations in the two unknowns ${x_{1s}}^2$ and ${x_{2s}}^2$. Their solution is given by (7).

Equations (B1) also can be used to obtain alternative expressions for b_1 and b_2 in (4). After some algebraic manipulation, (4) becomes

$$\text{(B2)} \quad y = y_s + b_{11}({x_1}^{\alpha_1} - {x_{1s}}^{\alpha_1})^2 + b_{12}({x_1}^{\alpha_1} - {x_{1s}}^{\alpha_1})({x_2}^{\alpha_2} - {x_{2s}}^{\alpha_2}) + b_{22}({x_2}^{\alpha_2} - {x_{2s}}^{\alpha_2})^2,$$

where y_s is the value of y at (x_{1s}, x_{2s}). When $b_{11} \neq 0$, (B2) is algebraically equivalent to

$$\text{(B3)} \quad y = y_s + \frac{1}{b_{11}}\left[{b_{11}}^2\left(z_1 + \frac{b_{12}}{2b_{11}} z_2\right)^2 + c{z_2}^2\right],$$

where $z_i = {x_i}^{\alpha_i} - {x_{is}}^{\alpha_i}$ (for $i = 1$ or 2). This shows that when $c > 0$, y takes a value which is (i) y_s or larger when $b_{11} > 0$, or else (ii) y_s or smaller when $b_{11} < 0$. Consequently the critical point is a minimum when $c > 0$ and $b_{11} > 0$ and a maximum when $c > 0$ and $b_{11} < 0$. When $c < 0$, the bracketed expression in (B3) is zero at (x_{1s}, x_{2s}), positive on the line $z_2 = 0$ (i.e. $x_2 = x_{2s}$), and negative on the curve

$$z_1 + \frac{b_{12}}{2b_{11}} z_2 = 0.$$

This alternation between positive and negative values characterizes a saddle point. When $b_{11} = 0$, (B3) no longer applies, but a simpler proof from (B2) shows that (x_{1s}, x_{2s}) is a saddle point. (In this case $c < 0$; we still disallow $c = 0$.)

Appendix C. Path of Joint Optimality

The problem of joint optimality, in principle, can be solved by derivative methods using Lagrange multipliers, and a system similar to (B1) can be obtained. Unfortunately, it involves two distinct sets of exponents (α_1, α_2), and, consequently, cannot be regarded as a linear system like (B1). However, the nonlinear search methods described in Appendix A can be used to maximize the two-variable function $y_a(x_1, x_2)$ subject to the constraint

$$\text{(C1)} \quad y_b(x_1, x_2) = C,$$

for some prescribed constant C.

To apply the search algorithm, it is necessary to replace the exact constraint (C1) by the inequality

$$\text{(C2)} \quad y_b(x_1, x_2) \geq C.$$

For examples in this paper, the constraints (C1) and (C2) always give the same result because, in the region of interest, y_a decreases as y_b increases, so that a maximum for y_a is achieved on the boundary of the region (C2). The constrained problem thus can be solved by maximizing the composite function

$$Y(x_1, x_2) = \begin{cases} y_a(x_1, x_2), \text{ if } y_b(x_1, x_2) \leq C, \\ y_a(x_1, x_2) - P[y_b(x_1, x_2) - C]^2, \text{ otherwise,} \end{cases}$$

where P is a larger penalty constant. All joint optima reported here were obtained in this way, using the Nelder–Mead simplex search described in Appendix A. Because the algorithm actually finds minima, Y was maximized by minimizing $-Y$.

Theoretically, points of joint optimality also could be found by maximizing the linear conbination

$$Z(x_1, x_2) = w_a y_c(x_1, x_2) + w_b y_b(x_1, x_2),$$

with prescribed constant weights w_a and w_b. This method was tried also, but it led to serious numerical instabilities that could be avoided by use of the function Y.

A Methodology for Estimating Area Fished for Baited Hooks and Traps Along a Ground Line

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The methodology that estimates area fished for baited hooks or traps involves experimental fishing of strings of baited hooks or traps at different spacing along a ground line. This methodology enables expansion of catch per effort to a population estimate, when other methods may be impracticable. Experimentation and estimation procedures are given and the method is applied to data for prickly sculpin (*Cottus asper*), halibut (*Hippoglossus stenolepis*), and sablefish (*Anoplopoma fimbria*).

Key words: baited hook, baited trap, stock assessment, fish density, longline, estimate

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Une méthode permettant d'estimer la superficie pêchée par des hameçons ou des casiers appâtés comporte une pêche expérimentale à l'aide d'une série d'hameçons ou de casiers appâtés échelonnés sur une ligne de fond. Grâce à cette méthode, il est possible de déduire une estimation de population à partir des prises par effort, dans les cas où les autres méthodes ne peuvent s'appliquer. Nous décrivons dans l'article qui suit les méthodes d'expérimentation et d'estimation, que nous illustrons à l'aide de données sur le chabot piquant, le flétan et la morue charbonnière.

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SEVERAL fishing methods utilize bait to attract fish to a capturing device. Such baits are usually deployed at equal distances along a ground line. Baited traps or hooks are commonly used in fisheries for halibut (*Hippoglossus stenolepis*), cod (*Gadus* sp.), sablefish (*Anoplopoma fimbria*), and benthic decapod crustaceans such as crabs, shrimps, crayfish, and lobster. Assessment may be a major problem for these fishery resources.

An assessment can be made if data on catch and effort from a fishery are available over a period of several years, provided the levels of effort vary considerably, but even in this favorable situation there are problems as pointed out by Butler and McDonald (1979).

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If the variations in effort are not great enough, or the time period of data too short, or the catching is not done commercially, population estimates can be made in the context of a research program using mark recapture methods or extrapolation of catch per effort and volume or area fished for acoustic or net sampling methods. Mark recapture methods are prohibitively expensive for some populations and acoustic methods are not suitable for assessment of demersal fishes. Net sampling methods cannot be applied in many situations, particularly in lakes, reservoirs, and continental shelf areas where bottom relief or debris prohibit operation of nets. To estimate stock size directly from catches of baited hooks or traps it is necessary to estimate the area fished by such a device.

The following method was originally proposed by Rickard (1980) for estimating the area fished for capturing devices

deployed at equal distances along a ground line. We assumed that each capturing device has on the average a circular capturing field of fixed radius and if a fish occurs within the capturing field, it is caught by the gear. The method involves fishing experimentally lines of trapping devices, each spaced at different distances. If the spacing distances are small, the capturing fields will overlap. The amount of overlap increases as the spacing distance along the ground line decreases, resulting in declining catch per capturing device.

Theory

Let A = area of a single capture field, T = total area of N overlapping capture fields along the ground line, R = radius of single capture field, X = distance between adjacent devices along the ground line, and L = area of overlap of two adjacent capture fields. If the target species of the gear is located on or near the bottom, then the combined capture field of the string of capture devices is equal to N nonoverlapping subareas (Fig. 1) that consist of $N - 1$ subfields of area $A - L$ and 1 field of area A. Therefore,

$$(1) \quad T = (N - 1)(A - L) + A = NA - (N - 1)L$$

The average capture area of an individual capture device in an overlapping configuration (B) is

$$(2) \quad B = \frac{T}{N} = A - \frac{N - 1}{N}L$$

Consider two adjacent capture fields of equal radius R at X distance apart ($X \leq 2R$) (Fig. 1). If the area of the sector FDE is S and the area of the triangle DEF is V, then the area of the intersection of the two adjacent capture fields (L) is

$$(3) \quad L = 2(S - V)$$

Now if Y = length of the base of triangle DEF (EF), and θ = angle FDE, then

$$(4) \quad S = \frac{\theta}{2\pi}(\pi R^2)$$

$$(5) \quad V = \frac{1}{4}YX$$

By the Pythagorean theorem

$$(6) \quad Y = 2\left(R^2 - \frac{X^2}{4}\right)^{1/2}$$

Combining eqs. (5) and (6)

$$(7) \quad V = \frac{X}{2}\left(R^2 - \frac{X^2}{4}\right)^{1/2}$$

To find θ,

$$\cos\left(\frac{\theta}{2}\right) = \frac{X}{2R}$$

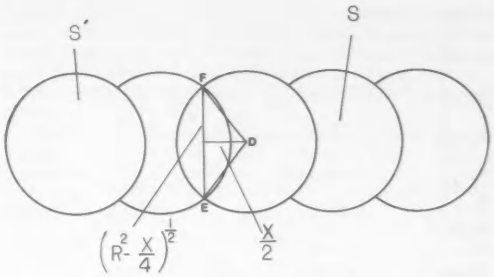

FIG. 1. Intersection of N circular capture fields and the geometry of the area of intersection between two adjacent fields.

Thus

$$(8) \quad \theta = 2\cos^{-1}\left(\frac{X}{2R}\right)$$

combining eqs. (3), (4), (7), and (8)

$$(9) \quad L = 2\left[\cos^{-1}\left(\frac{X}{2R}\right)R^2 - \frac{X}{2}\left(R^2 - \frac{X^2}{4}\right)^{1/2}\right]$$

The average area of the capture field relative to the area of a solitary capture field (C) is

$$(10) \quad C = \frac{B}{A} = 1 - \frac{KL}{\pi R^2}$$

where

$$K = \frac{N - 1}{N}$$

Substituting eq. (9) into eq. (10) gives

$$(11) \quad C = 1 - \frac{2K\left[\cos^{-1}\left(\frac{X}{2R}\right)R^2 - \frac{X}{2}\left(R^2 - \frac{X^2}{4}\right)^{1/2}\right]}{\pi R^2}, \qquad (X \leq 2R)$$

Equation (11) depends on both X and R but may be transformed to a single variate by defining

$$Z = \frac{X}{2R}$$

$$(12) \quad C = 1 - \frac{2K\cos^{-1}(Z)}{\pi} + \frac{2KZ}{\pi}(1 - Z^2)^{1/2}$$

This simplifies our model. C is defined on the interval 0 to 1 (Fig. 2) or equivalently X is defined on the interval 0 to $2R$. If X is greater than $2R$, the capture fields do not overlap and no competition for fish occurs among adjacent capture devices. The first derivative of C as given by eq. (12), which

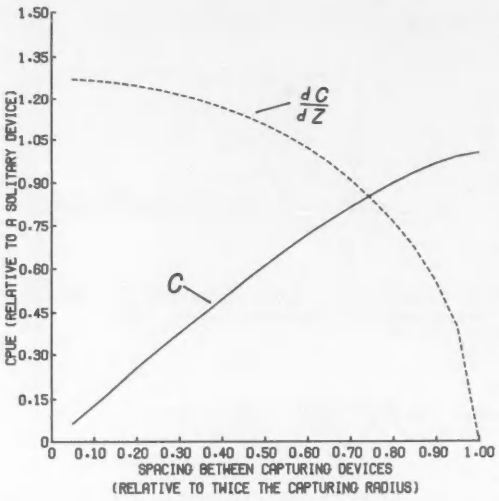

FIG. 2. Catch per capturing device and its first derivative as a function of the spacing between capturing devices.

can be useful in the estimation procedure outlined below, is

$$\frac{dC}{dZ} = \frac{4K}{\pi}(1 - Z^2)^{1/2}$$

Estimation of the Radius of the Capturing Field

The radius of the capturing field may be estimated from an experiment that measures the response of catch per capturing device to spacing of the capturing devices along the ground line. In the experiment several strings of devices at different spacings are fished simultaneously. The expected catch per device is

$$(13) \quad E(U_i) = C_{\max}C_i$$

where $E(U_i)$ = expected catch per device of the ith sampling unit, $C_{\max}$ = maximum catch per device, and C_i = area of the capturing field for the ith spacing distance (relative to that of a solitary device) (given in eq. (11)).

$C_{\max}$ depends on the density of fish in the fishing area as well as the soak time and assumes independence among strings of devices. In the experiment, soak time must be uniform among sampling units and of short enough duration so that gear saturation is negligible. If the latter condition is not met, gear saturation will mask the effect of competition among capturing devices. The length of soak for which gear saturation is negligible can easily be determined by an experiment with a single capturing device operated for several soak times. Ideally $C_{\max}$ would represent that portion of the population within the capturing field. If some members of the population in the capturing field are not caught, then the population estimate by this procedure is a lower bound for the true population value.

The procedure requires observations over a broad spectrum of hook spacings to ensure nonoverlap of capturing fields for some experimental units. $C_{\max}$ can be estimated from the nonoverlapping experimental units. A zero intercept line approximates the theoretical relation for overlapping experimental units. The approximate model may be estimated by standard linear regression. The point at which the estimated catch per device equals $C_{\max}$ provides the estimate of the radius of the capturing field (Rickard 1980).

A more formal procedure for estimating R involves nonlinear least squares. As a closed form analytical model for $E(U_i)$ with continuous first derivative is available, several iterative least-squares methods may be applied. The simplest of these, the Taylor series method (Spang 1962; Glass 1967), worked well for estimation of R. The method is superior to the linear regression method because it estimates R and its variance directly.

The expected catch per capture device must be defined differently for $X_i \leq 2R$ and $X_i > 2R$, because eq. (11) is undefined for $X_i > 2R$.

If $X_i \leq 2R$

$$U_i = C_{\max}\left(1 - \frac{2K}{\pi R^2}\left[\cos^{-1}\left(\frac{X_i}{2R}\right)R^2 - \frac{X_i}{2}\left(R^2 - \frac{X_i^2}{4}\right)^{1/2}\right]\right)$$

If $X_i > 2R$

$$U_i = C_{\max}$$

The Taylor series method is an iterative procedure for finding the parameter value $(\hat{C}_{\max}, \hat{R})$ that minimizes the sum of deviations squared:

$$\Sigma(Y_i - U_i)^2$$

where Y_i is the observed and U_i is the predicted catch per device at the ith spacing (X_i).

The Taylor series method, in some cases, does not converge. This problem has led to the development of alternative methods (Marquardt 1963; Conway et al. 1970). Note that both the Taylor series and Marquardt methods are available in some preprogramed packages of statistical procedures, such as SPSS (Robinson 1977; Nie et al. 1975). Approximate confidence intervals for parameters estimated by nonlinear least squares were given by Conway et al. (1970).

The treatment above applies to devices located on or near the bottom to capture organisms that may be considered as located on a two-dimensional surface. This obviously does not apply to pelagic fishes, for whom the capturing fields would be more appropriately represented as spheres rather than circles. The theory can be easily modified to handle this situation. By integral calculus it may be shown that the volume of overlap of two spheres of radii R whose centers are at a distance X apart is

$$\frac{4}{3}\pi R^3 - \pi\left(R^2X - \frac{X^3}{12}\right)$$

Then the average capture volume of N spheres with centers X apart (all spheres of radius R) relative to the solitary capture volume V_1 is given by

$$C = \bar{V}/V_1 = 1 - K\left[1 - \frac{3}{4}\left(\frac{X}{R}\right) + \frac{1}{16}\left(\frac{X}{R}\right)^3\right],$$

$$K = \frac{N-1}{N}$$

as defined earlier or defining

$$Z = \frac{X}{2R} \text{ as above}$$

$$C = 1 - K\left[1 - \frac{3}{2}Z + \frac{1}{2}Z^3\right]$$

Again with catches from strings of capture devices at different distances apart it is possible using nonlinear regression to estimate C_{max} and R.

Results and Discussion

Rickard (1980) originally applied the above method specifically to estimating abundance of prickly sculpin (*Cottus asper*) in Lake Washington. He fished pairs of baited minnow traps at various distances. The area of the minnow traps' capture field was estimated from the relation between trap spacing and catch per trap (Table 1). A large survey of Lake Washington was later conducted to measure catch per trap. These data were expanded to abundance based on the perceived area fished by the trap and the surface area sampled. Catches were adjusted to take into account selectivity of the gear, because it was clear that the ages younger than 4 were not fully vulnerable to the traps. Though a large number of assumptions were involved, in this way it was possible to estimate the total population at 2.112×10^8 fish of all ages, which revealed that prickly sculpin constituted the major biomass of fish in the lake, notwithstanding the presence of substantial numbers of sockeye salmon (*Oncorhynchus nerka*), threespine stickleback (*Gasterostens aculeatus*), longfin smelt (*Spirinchus thalerichthys*), yellow perch (*Perca flavescens*), peamouth (*Mylocheilus caurinus*), and others (Rickard 1980; Eggers et al. (1978). As prickly sculpin were not caught in large numbers with other sampling methods (gill net, midwater trawl) that were routinely applied previous to Rickard's study, the application of the minnow trap assessment provided a surprising perspective of the Lake Washington fish community.

This perspective has facilitated an interpretation of some observed changes in the Lake Washington zooplankton community (Edmondson 1979) following diversion of sewage treatment plant effluent from the lake. *Daphnia* appeared in the lake during 1974, 5 yr after the lake's nutrient regime had stabilized (Edmondson and Lehman 1981). The appearance of *Daphnia* occurred following the decline of its principal predator, *Neomysis mercedis* (Murtaugh 1981; Eggers et al. 1978). Prickly sculpin consumed *Neomysis* and were abundant enough to exert considerable predation on the *Neomysis* (Eggers et al. 1978). The vertical distribution of *Neomysis* had become deeper during the period of *Neomysis* decline. It was thought that the decline in *Neomysis* could be explained by the deeper vertical distribution, presumably in response to increasing water clarity accompanying improvement in the lake's water quality (Edmondson 1979), causing increased vulnerability to predation by prickly sculpin.

TABLE 1. Data from experimental fishing of strings of capturing device at different spacing, and results of fitting theoretical relation between spacing and catch per device. Given are parameter estimates and 90% confidence intervals. Halibut data from Hamley and Skud (1978); sablefish data from Sasaki (1979); sculpin data from Rickard (1980).

Target species	Gear	Catch (no./device)	Spacing (m)
Halibut	Longline	0.0348	2.74
		0.0393	3.81
		0.0410	5.49
		0.0504	6.40
		0.0421	7.32
		0.0561	10.97
		0.0623	12.80
	$\hat{C}_{max} = 0.055 \pm 0.051$; $\hat{R} = 3.94 \pm 6.42$		
Sablefish	Longline	0.162	1.82
		0.178	2.22
		0.198	2.86
		0.181	4.00
	$\hat{C}_{max} = 0.19 \pm 0.037$; $\hat{R} = 1.25 \pm 0.57$		
Prickly sculpin	Minnow trap	1.967	0
		1.967	0.91
		3.00	1.83
		2.133	2.74
		2.867	3.66
		3.067	4.57
		2.60	5.49
		2.967	6.40
	$\hat{C}_{max} = 2.97 \pm 2.78$; $\hat{R} = 2.01 \pm 9.34$		

Results of experimental fishing of halibut longline gear of various hook spacings were reported by Hamley and Skud (1978). The observed pattern of catch per hook relative to hook spacing (Table 1) was very similar to that predicted by the above theory. A limited amount of data on catch per hook versus hook spacing are available for sablefish (Sasaki 1979). The Taylor series method was applied to each of these sets of data (Table 1, Fig. 3), resulting in estimates of 48.8 m^2 and 4.9 m^2 of bottom area fished per hook for halibut and sablefish, respectively.

An estimate of abundance of halibut was available from cohort analysis of the halibut fishery (Terrence J. Quinn III, International Pacific Halibut Commission, Seattle, WA, unpublished information). This was compared with estimates based on extrapolation of the mean catch per hook in the fishery, area fished per hook, and the total continental shelf area between 36.6- and 183.3-m depth contours (Table 2). The latter estimates of abundance were 18–31 times those based on cohort analysis. The overestimate was presumably due to the fact that fishermen target the placement of gear in areas that traditionally yield the highest catches. Use of fishery catch per effort in this way gives a highly biased estimate of stock density. Using random placement of effort in such a large survey area would give much lower estimates of stock

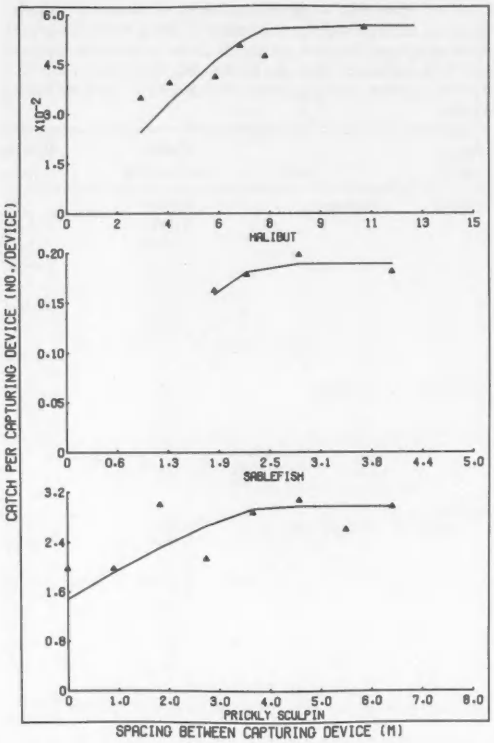

FIG. 3. Results of fitting by nonlinear least squares the theoretical relation between capturing device spacing and catch per capturing device for halibut, sablefish, and prickly sculpin.

density.

The method proposed here for estimating area fished by traps and hooks enables their use, in some circumstances, as resource assessment tools. Resource assessment methods that extrapolate catch per effort to density based on area or volume fished by the gear have been most highly developed for trawls (Houser and Dunn 1967; Alverson and Pereyra 1969) and for hydroacoustic gear (Cushing 1973; Forbes and Nakken 1972). Treschev (1978) has suggested that these methodologies may be developed for most fishing gears. However, to date there have been few applications to fishing gear other than hydroacoustics and trawls in resource assessment. This is due to problems with estimating and maintaining constant area or volume fished, as well as estimating gear efficiency and selectivity (Hamley 1975).

The halibut example discussed earlier showed one of the problems that can occur in extrapolating estimates from sample catches to the total population; namely, sampling is not random. Other problems could be created if there are currents which could greatly affect the distribution and concentration of the odor in the attracting field of baited hooks or traps. Depending on how currents are considered in the design of experiments to estimate area fished, currents at best contribute to the variance of density estimates and at worst contribute to bias of the resulting density estimates as well.

Another problem with this method is the possibility that the field of attraction of the baited hook or trap is not uniform over the area of capture. This might lead to the probability of capture of an animal decreasing with distance from the bait. In theory this could be handled if one knew or could assume the functional form of the decrease in capture probability with distance. In practice, there are two problems: even with a simple decay function, calculating the "effective" overlap area may be mathematically intractable, and even if it is tractable to work out the extension of the formula for C, it would introduce at best one additional parameter, thereby increasing the estimation problem. As is seen from Table 1 the confidence intervals for C_{max} and R can be extremely wide even with the simple model. To utilize a more complex model that would take into account a declining attraction with distance would require a substantially higher number of observations. Alternatively, separate experiments might be designed to measure such a decay function independently of

TABLE 2. Comparison of halibut abundance estimates in years when experimental fishing of longline gear occurred, based on area fished by a hook ($\hat{N}_2$) and cohort analysis (N_1).

Year	N_1[a] (millions)	Effort[b] (millions of hooks)	Catch per hook[b] (numbers)	N_2[c] (millions)	$\hat{N}_2/\hat{N}_1$
Halibut, Area 2, Northeast Pacific Coast, Willipa Bay, WA, to Cape Spencer, AK; area = 12.69×10^4 km^2					
1971	4.192	21.4	0.041	132.0	31
1972	4.110	22.1	0.033	106.2	26
1973	3.829	19.2	0.021	67.6	18
Halibut, Area 3, Gulf of Alaska, Cape Spencer to Shumagin Island; area = 26.37×10^4 km^2					
1971	6.596	30.3	0.028	187.3	28
1972	6.128	30.4	0.024	160.1	26
1973	5.725	29.4	0.016	107.0	19

[a]Abundance estimate based on cohort analysis of the halibut fishery (Terrance Quinn III personal communication).

[b]Data from Myhre et al. (1977), and estimates of mean weight of catch by area (Terrance Quinn III personal communication).

[c]Abundance estimate based on fishing; area per hook is 39.4 m^2. The figure based on 5.486-m hook spacing giving 80.8% of maximum possible area fished per hook (i.e. hook spacing greater than 7.880 m, and 39.4 m^2 = 0.808 (π(3.9 m)^2)).

the experiment to estimate C_{max} and R.

Both longline (Myhre 1969; Rollefsen 1953; Saetersdal 1963) and traps (Krouse and Thomas 1975; Parks 1973) are selective with respect to size of fish captured. Because large fish swim faster than small fish (in absolute distance traveled per unit of time) the effective trapping area of baited hooks and traps may be greater for larger fish. This problem may be taken care of by stratifying the catches in the experimental fishing by fish size, and thus deriving specific estimates per capture field area.

Escape from the hooks and traps probably occurs differentially with respect to fish size due to variable ratio of hook size to mouth size and entry port size to body girth. Certain segments of the population that have high escape rates would therefore be under represented in the catch. Without estimates of escape coefficients (based on the comparison of the size composition of the longline catches or trap catches to size composition of the population estimated independently) density estimates made with catch data from hooks or traps will be biased against those segments of the fish population for which the gear is selective.

Because of these difficulties, the method is likely to have practical applications where other approaches cannot be applied. With sufficient care and resources devoted to estimating area fished, the method can provide useful assessment of fish populations (e.g. in Lake Washington prickly sculpin). At the least, minimum population assessments may be made where intractable problems of efficiency or selectivity occur.

Acknowledgments

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Growth Patterns in a Newfoundland Atlantic Herring (*Clupea harengus harengus*) Stock

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MOORES, J. A., AND G. H. WINTERS. 1982. Growth patterns in a Newfoundland Atlantic herring (*Clupea harengus harengus*) stock. Can. J. Fish. Aquat. Sci. 39: 454–461.

Growth patterns in a discrete Atlantic herring (*Clupea harengus harengus*) stock were examined using back-calculated lengths derived from otolith measurements and empirical data. The influence of abiotic and biotic factors on growth was examined and evaluated for possible density-dependent or density-independent effects. The results give little evidence to support density-dependent herring growth in the 1st year, but suggest density-independent growth regulated by temperature. A growth compensation mechanism appears to occur in subsequent years resulting in a stable maturation pattern within the stock.

Key words: herring, growth, density-dependent, density-independent, growth compensation, maturation

MOORES, J. A., AND G. H. WINTERS. 1982. Growth patterns in a Newfoundland Atlantic herring (*Clupea harengus harengus*) stock. Can. J. Fish. Aquat. Sci. 39: 454–461.

Les caractéristiques de la croissance chez un stock indépendant de harengs de l'Atlantique (*Clupea harengus harengus*) ont été étudiées à l'aide de longueurs déterminées par rétrocalculs dérivés de mensurations d'otolithes et de données empiriques. Nous avons examiné l'influence de facteurs abiotiques et biotiques sur la croissance et les avons évalués en vue de détecter des effets possibles dépendants ou indépendants de la densité. Il y a très peu de preuve que la croissance du hareng dans sa première année soit dépendante de la densité, mais il y aurait plutôt croissance indépendante de la densité réglée par la température. Un mécanisme de compensation de croissance apparaît, semble-t-il, dans les années subséquentes, qui engendre des caractéristiques de maturation stables parmi le stock.

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TRADITIONAL fisheries studies tend to examine fish stocks in isolation assuming they are independent from other species and the physical environment. This approach was often necessitated by the constraints of the available data. As the data base has expanded in recent years, there has been renewed interest in examining the relationship of fish populations to their biotic and abiotic environment. Of particular interest has been the consideration of growth, maturation, and recruitment, and whether these are density-dependent or density-independent population characteristics (de Veen 1976; Lett et al. 1975; Lett and Kohler 1976; Winters 1976).

An examination of 1st year growth (l_1) in Atlantic herring (*Clupea harengus harengus*) by Lett and Kohler (1976) indicated an inverse relationship between l_1 and year-class size. They concluded that density-dependent growth in the 1st year determined subsequent growth thereby providing a population regulatory mechanism through the effect of growth on maturation determining the population fecundity. The control of adolescent herring growth by density-dependent effects during the 1st year of life, as postulated by Lett and Kohler (1976), precludes any subsequent influences such as density-independent effects of temperature, density-dependent effects through population biomass, or the effects of growth compensation. Unfortunately Lett and Kohler (1976) misinterpreted the conventions for the conversion of age (given in their data source (Messieh 1973)) to year-class resulting in the assignment of autumn-spawner year-classes 2 years too soon and spring-spawner year-classes 1 year too soon. When the year-classes were assigned correctly and the data replotted, a density-dependent relationship between 1st-year growth and year-class size could not be categorically demonstrated (Winters et al. 1977).

The elucidation of growth patterns in the Gulf of St. Lawrence herring is complicated by a variety of interacting factors. These include the many stock admixtures, the large and variable area occupied by the stock (Winters and Beckett 1978), the presence of two large (and perhaps interchangeable) spawning components within the stock, the dominance of two large year-classes which were produced under anomalous conditions after a major reduction of the stock biomass (Winters and Hodder 1975) by a fungus disease (Sinderman 1958), and the influence of a seasonal mackerel population (Moores et al. 1975). To determine what factors regulate growth in herring, we selected a small discrete stock of herring in Fortune Bay, Newfoundland (Fig. 1). This stock

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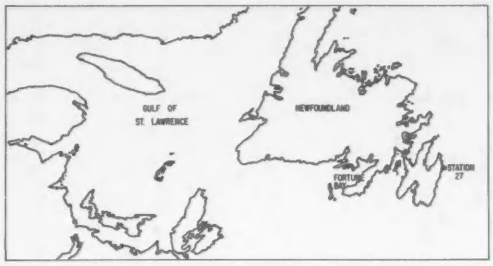

FIG. 1. Newfoundland and the Gulf of St. Lawrence showing location of Fortune Bay and Station 27.

has exhibited not only wide and frequent fluctuations in year-class success, but in combination with an intensive purse-seine fishery, has also shown large changes in overall abundance (Winters and Moores 1977). The situation is also simplified by the absence of any large amount of mackerel in the area, and the presence of only one major spawning component of herring (spring-spawners), which represent 90–95% of the total stock.

Methods and Materials

Otolith samples from each year-class (1958–74, excluding 1973) were selected from commercial samples of the Fortune Bay herring stock. All samples were selected from January to March, which represents the overwintering period during which growth would be minimal (Messieh 1969). Each otolith was drawn using a Wild M7 binocular microscope, equipped with a camera lucida, at a magnification of 25×. From the drawings, measurements were made of radius of first annulus (O_1), radius of second annulus (O_2), and total otolith radius (O_T) along an axis from the otolith center to the edge of the postrostrum (Fig. 2).

The relationship between otolith radius and fish length was examined using fish ranging in age from 1 to 8 yr old and in length from 84 to 363 mm. Age-groups 2–8 were represented by 25 fish each with 50 fish selected from age-group 1. All fish were from the 1968 year-class with the exception of age-group 1 which included individuals from the 1966 year-class.

To minimize the possible influence of Lee's phenomenon (Lee 1920) on the back-calculated length values, a standard age (age-group 5) was selected for examination. In several weak year-classes, however, insufficient material was available at this age necessitating the inclusion of several age-groups in the sample. Average O_1 values were calculated for each year-class, and separately for each age-group within the year-class.

Temperature data used in these analyses are mid-monthly surface temperatures from Station 27 (47°32′50″ N, 52°35′10″ W) which is located off St. John's Newfoundland. Although these temperatures are not from the exact area under examination, they should adequately reflect temperature trends in Fortune Bay because the Labrador current is the major component affecting both areas.

Maturity ogives were constructed from commercial sampling data broken down by length and age into mature and immature specimens. Maturity stages were assigned according to the eight-point scale recommended by the Herring Working Group of ICES (Anon. 1962) with stages 1 and 2 classified as immature and stages 3–8 as mature. The point of 50% maturity was determined by probit analysis.

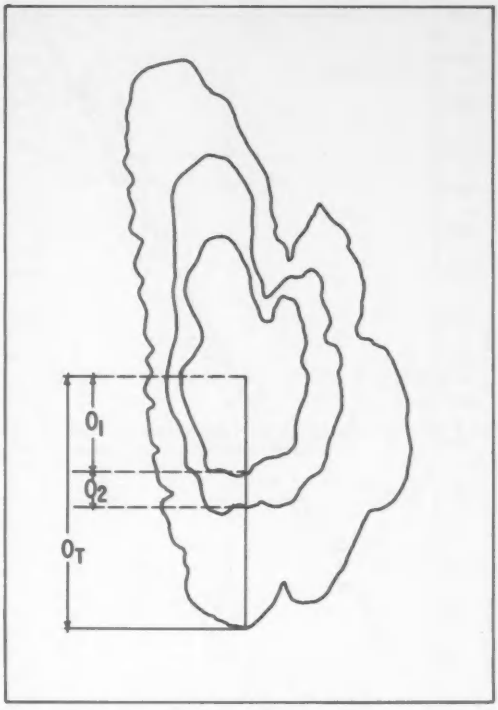

FIG. 2. Otolith measurements taken for back-calculation.

Estimates of year-class strength (at age 2) were derived by cohort analysis with $M = 0.2$ and starting $F = 0.1$ selected from an analysis of fishing effort and fishing mortality for 1967–73 (Winters and Moores 1977).

Results

Derivation of Otolith Radius–Fish Length Relationship and l_1 Values

Examination of the relationship between otolith radius and fish length (Fig. 3) shows a positive linear relationship ($r = 0.97$) indicating that the otolith radius accurately reflects fish length. The regression equation derived from the otolith radius–fish length relationship was then used to convert each O_1 value to a length-at-age 1 (l_1) value. This method estimates l_1 values without using the proportionatility technique (Lea 1919) which is heavily influenced by the observed length.

Because of the inclusion of several age-groups in the sample from weak year-classes, the influence of age on back-calculated length at age 1 was examined. Data were available for age-groups 5–8 from four year-classes (1962, 1965,

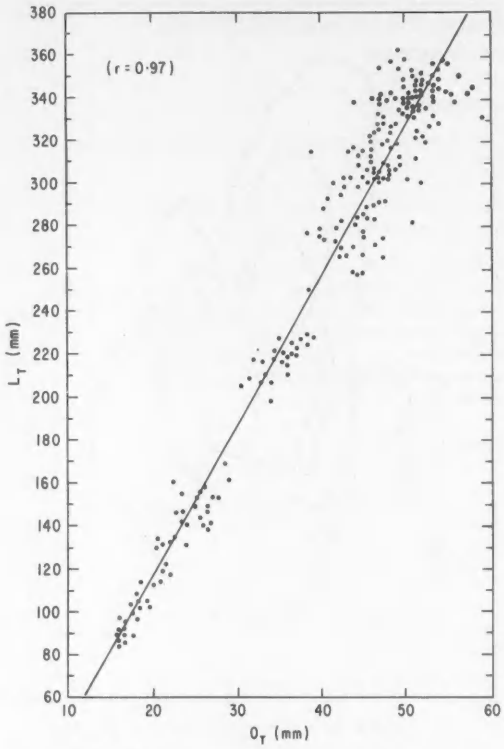

FIG. 3. Relationship of total otolith radius (O_T) to observed total length (L_T) (L_T = 69.82 O_T − 22.63). O_T measurements are from drawings at a magnification of 25×.

1966, and 1968). A plot of average l_1 at age for these year-classes (Fig. 4) shows no trend in l_1 with age, and therefore no adjustment by age was required. Where more than one

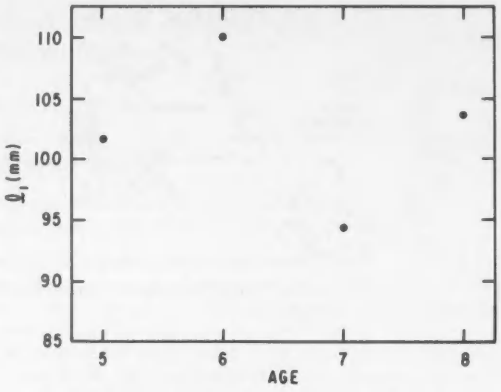

FIG. 4. Relationship of l_1 and age in Fortune Bay herring.

age-group was present in a sample the O_1 values were averaged over all ages and a single l_1 value was derived for each year-class (Table 1).

EFFECTS OF TEMPERATURE AND YEAR-CLASS SIZE ON 1ST-YEAR GROWTH

Day (1957) demonstrated a relationship between temperature and growth for Northwest Atlantic herring. This relationship was tested for the Fortune Bay herring stock using the mean monthly surface temperature summed (TEMPSUM) over the May−December period (time period available for growth in the 1st year (Table 1) and the back-calculated l_1 values). The data (Fig. 5) showed that l_1 size was positively correlated with temperature (r = 0.71).

Lett and Kohler (1976) postulated that 1st-year growth was affected by year-class size in a density-dependent manner. This was examined using both the calculated l_1 values and l_1 values adjusted to an arbitrary TEMPSUM signal of 60°C (Table 1). This adjustment was performed using the difference between the predicted l_1 at 60°C TEMPSUM and the

TABLE 1. l_1, temperature, and year-class size data for Fortune Bay herring.

Year-class	N	l_1 (regression O_T vs. L_T)	l_1 (adj. in 60°C)	TEMPSUM (May−Dec.)	Year-class size ($\times 10^{-6}$)
1958	47	97.5	102.7	57.1	16.5
1959	50	91.2	101.5	54.2	21.0
1960	50	118.4	117.3	60.6	13.7
1961	14	124.0	116.0	64.5	4.3
1962	15	121.9	127.6	56.8	3.4
1963	50	112.8	120.1	55.9	274.9
1964	50	105.8	115.9	54.3	3.5
1965	36	104.4	112.8	55.3	5.9
1966	50	96.1	103.7	55.7	136.8
1967	50	108.6	98.1	65.9	29.4
1968	49	84.9	96.6	53.4	149.1
1969	18	108.6	112.9	57.6	3.0
1970	28	118.4	108.1	65.8	5.1
1971	50	125.4	118.7	63.8	9.6
1972	25	100.3	115.7	51.3	7.6
1974	25	96.1	111.4	51.4	44.3

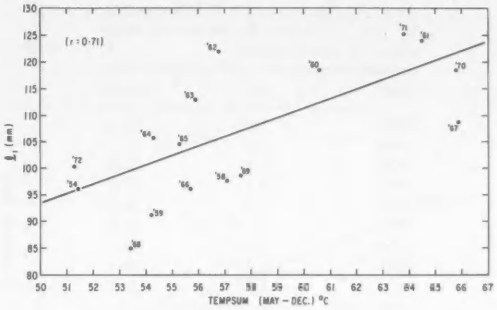

FIG. 5. Regression of TEMPSUM (May–December, Station 27) against l_1 of herring from Fortune Bay.

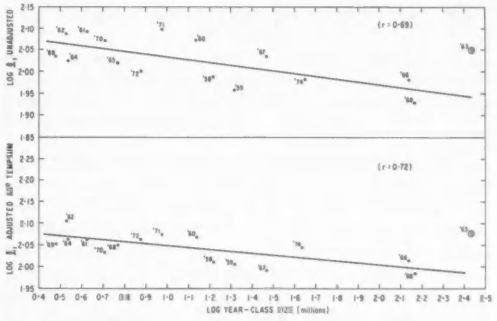

FIG. 6. A comparison of year-class size and l_1 unadjusted for temperature and adjusted for temperature (the 1963 value has been omitted from the regression).

predicted l_1 for the TEMPSUM for each year-class. In both cases, when the data were plotted there appeared to be an indication of curvilinearity. This was removed using a log–log transformation (Fig. 6). Using all data points gave a poor correlation ($r = 0.51$ for the unadjusted l_1 and $r = 0.44$ temperature-adjusted l_1). The 1963 data point appeared anomalous, and when removed the correlation improved to $r = 0.69$ for the unadjusted l_1 and to $r = 0.72$ for the temperature-adjusted values. A multiple regression of unadjusted l_1 values temperature and year-class size (omitting the 1963 value) gave an $r^2 = 0.63$ for temperature and l_1 increasing to 0.79 with the inclusion of year-class size.

Effects of Growth Compensation, Temperature, and Biomass on Subsequent Growth

Lett and Kohler (1976) have hypothesized that 1st-year growth of herring is the main determinant of a cohort's subsequent growth rate; this implies that the 1st-year growth (l_1) of a cohort should be well correlated with its subsequent age-specific lengths. This relationship between l_1 and l_T was examined for the 1968 year-class for which extensive sampling data were available. The results (Fig. 7) indicated that while length at age 2 was significantly correlated ($r = 0.77$) with l_1, the relationship was not statistically evident at ages 3,

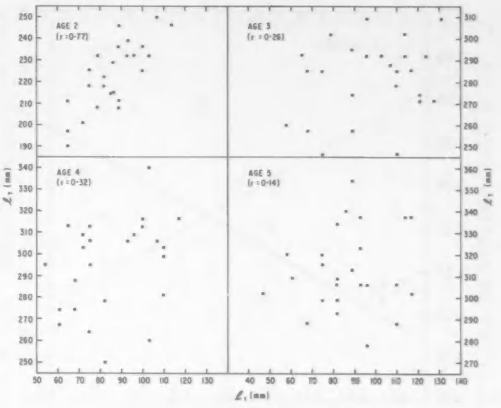

FIG. 7. Back-calculated length at age (l_T) for ages 2, 3, 4, and 5 and back-calculated l_1 for Fortune Bay herring.

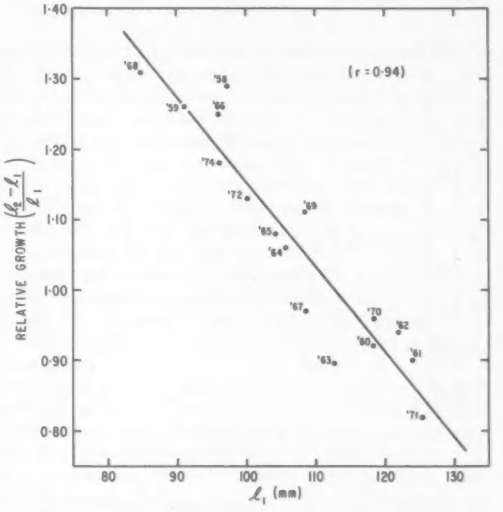

FIG. 8. A comparison of the relative growth rates and l_1 for Fortune Bay herring.

4, and 5. This suggests that other factors such as growth compensation, environmental variability, and logistic responses may have a much greater impact on life history growth patterns of herring than size attainment at the end of the 1st year.

Growth compensation in Fortune Bay herring was evaluated by comparing the relative growth rate ($RG = l_2 - l_1/l_1$) for age 2 to the back-calculated size at the end of the 1st year. The data (Fig. 8) showed a good correlation ($r = 0.94$) with a negative slope indicating the presence of a growth compensation mechanism which could act to ameliorate the effect of l_1 on subsequent growth.

Mean length-at-age data were available from commercial

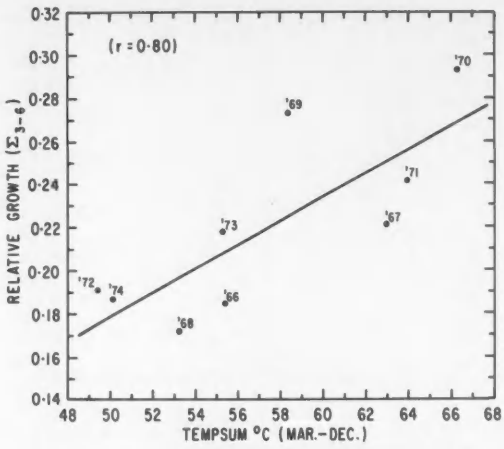

FIG. 9. The relationship between growth of Fortune Bay herring and Station 27 temperatures (TEMPSUM March–December).

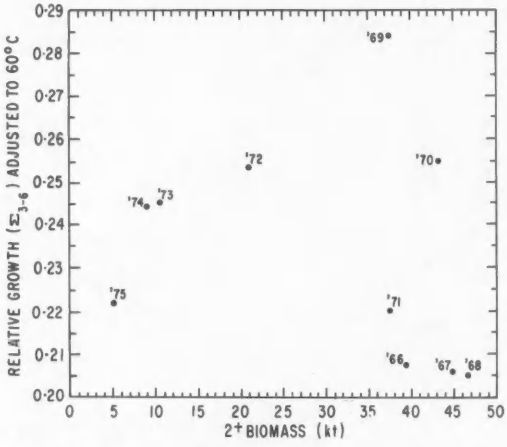

FIG. 10. The relationship of relative growth, adjusted to 60°C, and stock biomass (ages 2+) of Fortune Bay herring.

and research sampling activities for Fortune Bay herring for 1966–76. From these data relative annual growth, adjusted for length-dependent bias (Iles 1967), was computed for age-groups 3–6, representing not only the critical growth phase of this stock, but also an age-range associated with accurate age determination. While the growth period in the 1st year is restricted by hatching time, growth in subsequent years would cover a more extensive period. The relative growth of age-groups 3–6 (summed annually) was therefore compared to Station 27 TEMPSUM from March to December thereby including the major feeding period (Fig. 9). Correlation analyses indicate a significant positive relationship ($r = 0.80$) between temperature and growth during the adolescent age-range.

TABLE 2. Age and length of 50% maturity, by year, of Fortune Bay herring as determined by probit analysis.

Year	Age	Length
1968	3.5	26.8
1969	3.3	27.0
1970	3.2	26.9
1971	3.1	27.7
1972	2.9	26.9
1973	3.1	27.3
1974	2.6	26.5
1975	3.2	28.1
1976	3.3	26.6

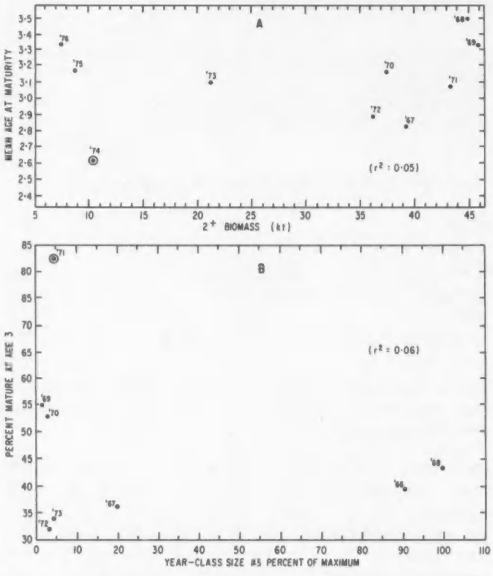

FIG. 11. The influence of population density on maturation of Fortune Bay herring. A. Mean age of maturity versus 2+ biomass (lagged by 1 yr). B. Percent mature at age 3 vs. year-class size.

Using the relationship shown in Fig. 9, the relative annual growth (age-groups 3–6) has been adjusted to values corresponding to a standard temperature of 60°C. These transformed values have been plotted against the 2+ biomass of Fortune Bay herring in Fig. 10. Correlation analyses suggest that growth of Fortune Bay herring has not been significantly ($r = 0.23$) affected by its population density during 1966–75.

MATURITY

Maturity data for Fortune Bay herring were available for 1968–76. Variation in the point of 50% maturity, calculated using probit analysis, was small and did not appear to follow a consistent pattern (Table 2).

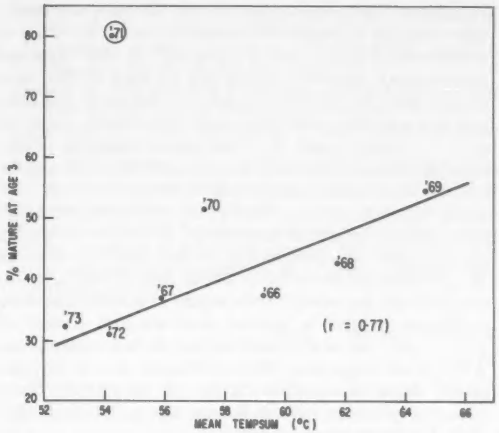

FIG. 12. Relationship of maturity in Fortune Bay herring by year-class to mean TEMPSUM (2 yr previous). The 1971 point has been excluded from the analysis as this sample was obtained in a catch from a spawning school.

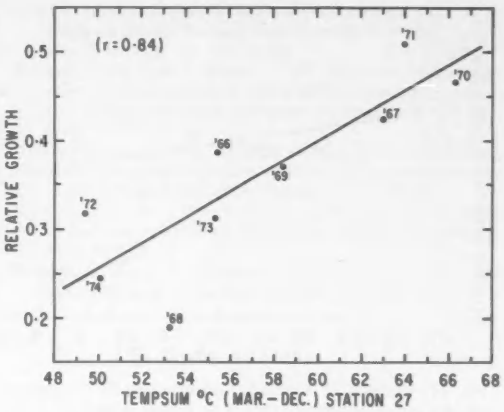

FIG. 13. Relationship of the combined relative growth rate of spring- (age-groups 3–5) and autumn-spawners (age-groups 4–6) from the southern Gulf of St. Lawrence herring stock to Station 27 TEMPSUM (March–December).

Large fluctuations in biomass levels and year-class strength such as those observed in Fortune Bay herring during 1966–76 (Winters and Moores 1977) have sometimes been associated with logistic changes in maturation rate and hence, population fecundity (Lett et al. 1975; de Veen 1976). Maturation rate data of Fortune Bay herring are plotted against population biomass (1-yr lag) and year-class size in Fig. 11A and B, respectively. Correlation analyses suggest that density-dependent changes in maturation rate are not significant factors determining relative changes in population productivity of Fortune Bay herring.

The effect of temperature (mean of the previous 2 years TEMPSUM) as an environmental signal affecting the maturation rate (expressed as % mature at age-group 3) of Fortune Bay herring is shown in Fig. 12. Exclusion of the 1971 year-class (age-group 3 in 1974) data point results in a highly significant positive correlation suggesting that temperature, through its effect on growth, is the major factor determining the maturation rate of this herring stock. The 1974 sample was obtained from schools of mature and/or maturing herring near the spawning area and thus would be expected to be biased towards the mature component of that year-class.

Discussion

Burd (1962) has hypothesized that the length of herring at the end of the 1st year's growth results in substantial length differences later in life. Lett and Kohler (1976), from analyses of southern Gulf of St. Lawrence herring, further argued that l_1 growth, but not subsequent growth, is density-dependent and acts as the only natural means for regulating a stock through its population fecundity, with the age of maturation being determined by the l_1 size. This implies that density-independent factors such as temperature, and intrinsic factors such as growth compensation, have minimal effects on population growth dynamics.

Analyses of growth data of Fortune Bay herring presented in this paper do not support the above hypotheses. On the contrary, these analyses suggest that density-independent processes mediated through an environmental signal (temperature) act to regulate not only l_1, but also subsequent growth, to the extent that maturation rate and length-at-age of a year-class are not measurably affected by density or the size attained at the end of the 1st year. Winters et al. (1977) reached a similar conclusion regarding the density-dependence of l_1 size from a reanalysis of the southern Gulf data presented by Lett and Kohler (1976). However, from correlation of trends in size and population biomass, Winters (1976) concluded that growth of adolescent (age-groups 3–7) herring in the southern Gulf was density-dependent with changes in growth also being affected (to a lesser degree) by fluctuations in mackerel abundance. Because of the lack of a complete temperature time series of the southern Gulf, temperature effects on growth were not evaluated by Winters (1976). The Station 27 temperature data, however, correlate well ($r = 0.71$) with those available from the southern Gulf (Lauzier and Hull 1969; W. T. Stobo, Department of Fisheries and Oceans, Halifax, N.S., personal communication) and may be taken as representative of hydrographic conditions in that area. Length-at-age data of southern Gulf herring given in Winters (1975) have been calculated as relative annual growth increments (summed over age-groups 3–7), and these are plotted against TEMPSUM (Station 27) in Fig. 13. Correlation analyses suggest that variations in annual growth of southern Gulf herring are attributable in large part to environmental changes, as exemplified by temperature. When the effects of temperature on growth are removed and the data regressed against 2+ herring biomass (Fig. 14), a weak density-dependent growth response becomes evident. Furthermore, the addition of juvenile mackerel (age-groups 1 and 2) biomass (which are in the same size range as 3- to 7-yr-old herring) tends to intensify the logistic growth response in herring (Fig. 15). Multiple regression analyses indicate that the amount of explained variation in herring growth increased from 70.9% when temperature alone was considered to 82.6%

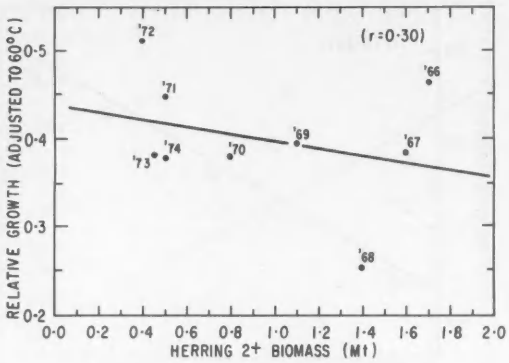

FIG. 14. Influence of herring 2+ biomass on the temperature-adjusted growth of southern Gulf of St. Lawrence herring.

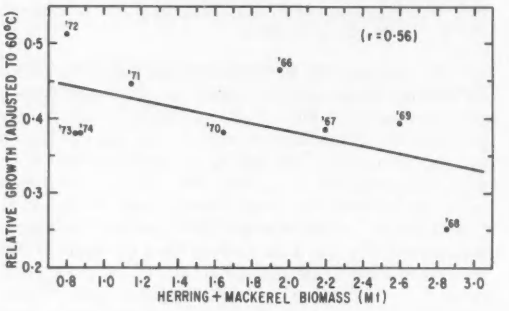

FIG. 15. Influence of combined herring and mackerel biomass on the temperature-adjusted growth of southern Gulf of St. Lawrence herring.

with the addition of juvenile mackerel biomass, and to 83.2% with the further addition of herring biomass. Thus it would appear that logistic growth patterns in this herring stock would only be evident under fairly stable environmental conditions.

The apparent absence of homeostatic growth mechanisms in Fortune Bay herring as opposed to southern Gulf herring is perhaps related to the more northerly location of Fortune Bay in relation to the environmental range of herring in the Northwest Atlantic (Leim and Scott 1966). Thus, not only would Fortune Bay herring be more susceptible to environmental variations than southern Gulf herring, but also the environmental variations themselves are probably greater in the Fortune Bay area than in the southern Gulf. For example, the coefficient of variation of summer temperature (June–September) for 1955–69 at Station 27 is 7.5% compared with 4.8% for Entry Island (Lauzier and Hull 1969). In a broader sense, the lower productivity and greater variability in year-class strengths of herring stocks in the Newfoundland area relative to those in the center of herring distribution in the Nova Scotia area (4X) are functions of environmental control, and the same environmental controls with similar variability would apply.

Hubold (1978) concluded that density-dependent growth occurred in North Sea herring and that the onset of maturity was a function of length. While analysis for the influence of environmental factors was not performed, the data suggested compensatory growth. Cushing and Dickson (1976), in a discussion of the match/mismatch hypothesis of year-class size determination, state that larger year-classes would be produced during years of cooler water conditions. Under these conditions it would follow that growth would also be slower. The resultant l_1 value and the size of the year-class would therefore both be a function of the environment rather than a density-dependent relationship. Similarities in herring growth have been observed by Tibbo (1957) for Gulf of St. Lawrence and Nova Scotia stocks, and by Saville (1978) for the North Sea stocks. Both authors concluded that these similarities suggest a general environmental control of growth, and this study lends support to their conclusions. While density-dependent factors influence growth to some extent, density-independent factors are the primary determinant of growth in both the Fortune Bay and southern Gulf of St. Lawrence herring stocks.

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Optimal Utilization of a Variable Fish Supply

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SILVERT, W. 1982. Optimal utilization of a variable fish supply. Can. J. Fish. Aquat. Sci. 39: 462–468.

Successful exploitation of a fishery depends not only on the quantity of fish caught and processed, but also on the steadiness of supply. Too much variability in catch means that supplies will sometimes be inadequate, while at other times there will be too many fish to process, and the market will become glutted. Fisheries managers must therefore be prepared to make a trade-off between maximization of mean yield and minimization of the variance of this yield if the fishery is to function optimally. To do this they must understand the economic trade-offs that enter into the catching, processing, and marketing aspects of the fishery. This paper presents a strategy for coupling biological and economic models and illustrates how these questions can be quantified and integrated to arrive at a bioeconomically optimal management strategy.

Key words: optimality, variability, fisheries management, sustainable yield

SILVERT, W. 1982. Optimal utilization of a variable fish supply. Can. J. Fish. Aquat. Sci. 39: 462–468.

Le succès de l'exploitation d'une pêche dépend non seulement des volumes de poissons capturés et transformés mais également de la régularité des approvisionnements. Si les prises accusent de trop fortes variations, les approvisionnements seront parfois inadéquats tandis qu'à d'autres périodes, il y aura trop de poisson à transformer, et le marché deviendra saturé. Les gestionnaires des pêches doivent donc être prêts à un compromis entre une maximisation du rendement moyen et une minimisation de la variance de ce dernier en vue du fonctionnement optimal de l'entreprise. Á cette fin, il leur faudra comprendre les compromis économiques qui caractérisent la capture, la transformation et le marketing dans l'industrie de la pêche. L'article qui suit décrit une stratégie visant à associer modèles biologiques et économiques, et illustre la façon dont ces questions peuvent être quantifiées et intégrées pour en arriver à une stratégie de gestion bioéconomiquement optimale.

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THERE is general agreement that the basic goal of fisheries management is to maximize the benefits to society from the fishery. It is difficult to pursue this goal directly, because it has many social, political, and economic ramifications; fish may be thought of as food, as dollars, as political bargaining counters, or as recreation. Fisheries management, therefore, is carried out by groups of specialists, and each group addresses itself to a set of secondary objectives related to the expertise of its members rather than to the primary objective of maximum social benefit. For example, biologists have traditionally been expected to recommend ways of maximizing the sustainable yield without questioning the optimality of this goal, and economists have been assigned the problem of turning this supply of fish into as many dollars and other social benefits as possible.

During the past decade there has been a growing awareness that this is an inefficient way of organizing fisheries management, and in particular that maximizing fish yield on a sustained basis is not necessarily the way to maximize benefits from the fishery. It can even be "optimal" in a strictly economic sense to overfish a stock to extinction, rather than maintain it at a sustained level of harvest (Clark 1973; Silvert 1977). The concept of maximum sustainable yield (MSY) has thus been replaced by that of optimum sustainable yield. A sophisticated mathematical theory for the calculation of the levels of optimum sustainable yield has been developed by Clark (1976) and others.

One problem with this approach is that it addresses the problem of optimality very well, but it does not deal with the problem of sustainability. Even in fisheries which have been managed on the basis of maximum sustainable yield for many years, the annual catches are variable and this poses serious problems for the industry. A very poor year may cause some fishermen and plants to fail to meet their fixed operating costs and can drive them out of business, while the benefits of a good year may not be realized if there is insufficient capacity to catch and process the available fish, or if market demand is so inelastic that the price falls drastically.

Fisheries managers have come to realize that maximum or

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optimum sustainable yield strategies tend to destabilize stocks, that variability can be greatly reduced by maintaining stocks at levels somewhat above those required for maximum yield (Ricker 1958; Allen 1973; Walters 1975; Doubleday 1976; Holling 1978), and some stocks are now managed at such levels. However, little effort has been directed at estimating the true costs of stock variability, and most of the arguments for stabilization of yield are based on biological rather than socioeconomic grounds. There is nothing wrong with this so long as the result is the same, but it seems surprising that the management of stocks in terms of variability as well as mean yield should derive entirely from biological arguments without consideration of what the costs of variability are to the industry as a whole.

This paper is intended to show that it is possible to couple a biological model of a fish stock which describes its variability to an economic model of the catching and processing of a variable stock in such a way that both the economic submodel and the entire bioeconomic model can be optimized. This type of approach should make it possible for government and industry economists to work with fisheries biologists to arrive at realistic secondary objectives which are more effective in directing the entire fishery towards its primary goal of maximizing the total social benefit in all of its many aspects.

Model of a Variable Fish Stock

There are many ways in which variability can arise in the population dynamics of a fish stock. This example uses a deterministic stock–recruitment model with uncertainty in the assessment process; the precise form of the model does not affect the basic form of the analysis. The particular model used here is made simple so that the coupling to the economic model is as clear as possible.

The recruitment in year t, R_t, is assumed to be a function of the parent stock in year $t-1$, P_{t-1}:

$$R_t = F(P_{t-1}).$$

If the parents die immediately after spawning and if natural mortality during the fishing season is neglected, then the parent stock in year t is equal to the number of recruits minus the yield Y_t,

$$P_t = R_t - Y_t.$$

A reasonable management strategy is to try to maintain the stock at a constant level so that the number of spawners after each season is a fixed value $\bar{P}$. If the stock could be assessed exactly, then there would be constant recruitment given by

$$\bar{R} = F(\bar{P})$$

and a constant yield

$$\bar{Y} = \bar{R} - \bar{P} = \bar{F}(\bar{P}) - \bar{P}.$$

If, however, the observed recruitment R_t^{obs} is in error by a random amount ϵ_t,

$$R_t^{\text{obs}} = R_t + \epsilon_t,$$

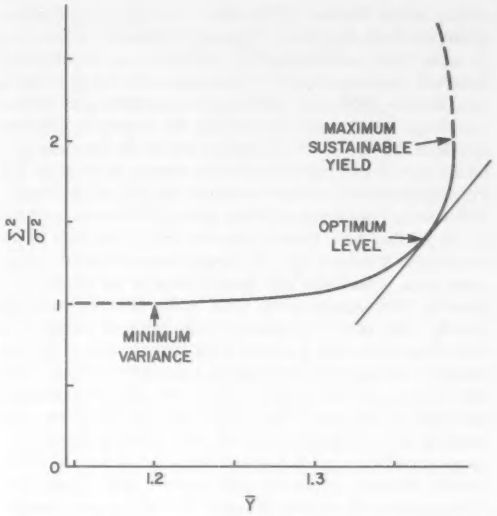

FIG. 1. Yield–variance relation for the Arcto–Norwegian cod stock. The tangent line is used to find the optimal management strategy; see text.

then the estimated yield for restoring the stock to equilibrium is in error by the same amount, namely

$$Y_t = R_t^{\text{obs}} - \bar{P} = R_t + \epsilon_t - \bar{P}.$$

The parent stock at the end of the season is given by

$$P_t = R_t - Y_t = \bar{P} - \epsilon_t,$$

and the recruitment the following year is

$$R_{t+1} = F(P_t) \approx F(\bar{P}) + F'(\bar{P})\epsilon_t$$

if ϵ_t is sufficiently small. Finally we obtain for the difference between Y_{t+1} and its equilibrium value the result

$$Y_{t+1} - \bar{Y} = R_{t+1} - \bar{R} + \epsilon_{t+1} \approx F'(\bar{P})\epsilon_t + \epsilon_{t+1}.$$

Thus if ϵ_t has mean 0 and variance σ^2, the mean yield from the fishery is $\bar{Y}$ and the variance is

$$\Sigma^2 = \text{var}(Y) = (1 + F'^2 + rF')\sigma^2$$

where r is the autocorrelation between ϵ_t and ϵ_{t+1}.

The relationship between mean yield and variance is illustrated in Fig. 1, based on a Ricker model of the form

$$R_{t+1} = \alpha P_t e^{-\beta P_t} t$$

with $r = 0$ and $\alpha = 6$, which is the value found for Arcto–Norwegian cod stocks (Garrod 1967; Ricker 1975). The solid part of the curve shows a region where a 20% increase in mean yield leads to a doubling in the annual variance of the catch, and the optimum management strategy lies in this

region, which Walters (1975) refers to as the Pareto frontier. Along the dashed sections of the curve simultaneous increase in mean yield and decrease in variability can be obtained; therefore optimum long-term strategies would not be found in these regions. However, with a high discount rate, the optimal sustainable yield could fall below the minimum variance threshold (Silvert 1977). The exact form of the curve depends on the recruitment model and the parameter values used, but the general pattern shown here should hold for all reasonably well-behaved stock–recruitment models. The main points to notice are that there exists a range of stock sizes over which an increase in mean yield can only be achieved at the cost of an increase in variance, and that the slope of the relationship between variance and mean yield varies between zero and infinity. The optimum balance point must lie somewhere along this curve, and it cannot correspond to one of the end points of this section. If we try to maintain the stock at the MSY level, we find that the slope of the curve is infinite at that point, which means that a finite reduction in variance can be achieved for negligible loss of yield. Similarly, the minimum variance end point is where the slope of the curve falls to zero; therefore a finite increase in yield could be obtained with almost no increase in variance. The biological submodel can thus be used to determine the limits of the optimum management strategy, but the optimum strategy itself depends on economic factors involved in the trade-off between mean yield and variability. To complete the analysis, we need to couple a biological submodel of the type shown here to an economic submodel of the fishing industry.

Processing a Variable Supply of Fish

The economic submodel described here is necessarily a simple one, because the trade-off between yield and variance involves a number of socioeconomic factors which vary from fishery to fishery. The time scale is also important, and the full benefits of a reduction in variability may take several years to manifest themselves. For example, fish marketing would be greatly improved if the industry could guarantee continuity of supply (Rabinovitch 1976), but the development of a marketing strategy and distribution mechanism to take advantage of such continuity is a long-term project. A realistic approach to the economic aspects requires starting with a simple model formulation based on current information and subsequent development of more sophisticated models which utilize the knowledge gained with increased stabilization of the fishery. In fact, it may even be desirable to try to overstabilize the fishery in order to assess the actual cost of variance in yield (Silvert 1978).

The economic model used here focuses entirely on processing capacity and is based on the assumptions that the amount of fish which can be processed and sold, S, cannot exceed the capacity C of the industry, i.e.

$$S = \min(Y,C)$$

and that all costs and prices associated with the industry are fixed; thus any returns to scale and elasticities of supply and demand are ignored. We also assume that the entire quota of fish must be caught, even if it exceeds the processing capacity; this assumption does not always hold, but it is not uncommon for plants to buy more fish than they need to maintain good relations with the fishermen. No allowance will be made here for options such as freezers to store excess catch until it can be processed or meal plants which turn excess fish into fodder.

The net return to the fishing industry is

$$R = aS - bY - cC = a\cdot\min(Y,C) - bY - cC$$

under these assumptions, where a is the income per unit of fish processed, b is the cost of the fish, and c is the cost of maintaining capacity C, including amortized capital costs. If $p(Y)$ is the probability of having yield Y in a given year, then the expectation value of R is

$$\begin{aligned}\langle R\rangle &= a\cdot\langle\min(Y,C)\rangle - b\langle Y\rangle - cC\\ &= a\left[\int_o^C Yp(Y)dY + \int_C^\infty Cp(Y)dY\right] - b\int_o^\infty Yp(Y)dY - cC\\ &= a\int_o^C Yp(Y)dY + \left[a\int_C^\infty P(Y)dY - c\right]C - b\int_o^\infty Yp(Y)dY.\end{aligned}$$

For a given $p(Y)$ the optimum capacity is therefore given by

$$\frac{\partial\langle R\rangle}{\partial C} = a\int_C^\infty p(Y)dY - c = 0.$$

Because

$$\frac{\partial^2\langle R\rangle}{\partial C^2} = -a\,p(C) < 0$$

this always corresponds to a maximum. The optimum capacity C_{opt} is therefore an implicit function of c/a, and the precise value depends on the probability function $p(Y)$; if Y has a normal distribution with mean $\bar{Y}$ and variance Σ^2, then

$$\int_C^\infty p(Y)dY = P(Y < C) = \frac{1}{2}\operatorname{erfc}\frac{C-\bar{Y}}{\Sigma\sqrt{2}} = \frac{c}{a}$$

for the optimal value of C, as shown in Fig. 2. The corresponding mean return is

$$\langle R\rangle_{\text{opt}} = (a-b-c)\,\bar{Y} - (a\Sigma/\sqrt{2\pi})\exp[-(C_{\text{opt}}-\bar{Y})^2/2\Sigma^2].$$

Thus the maximum mean revenue from the fishery depends in a complicated way on both the mean yield and the variance. However, it is easy to evaluate the result in several limiting cases. If c/a is very small, then the optimum capacity is much larger than $\bar{Y}$ and $\langle R\rangle_{\text{opt}} \approx (a - b - c)\,\bar{Y}$; we get the same result if Σ is very small. In both cases it is practical to have enough capacity to process all fish caught without paying a large amount for excess capacity. On the other hand, if $c/a = 1/2$, then $C_{\text{opt}} = \bar{Y}$ and the supply of fish can be ex-

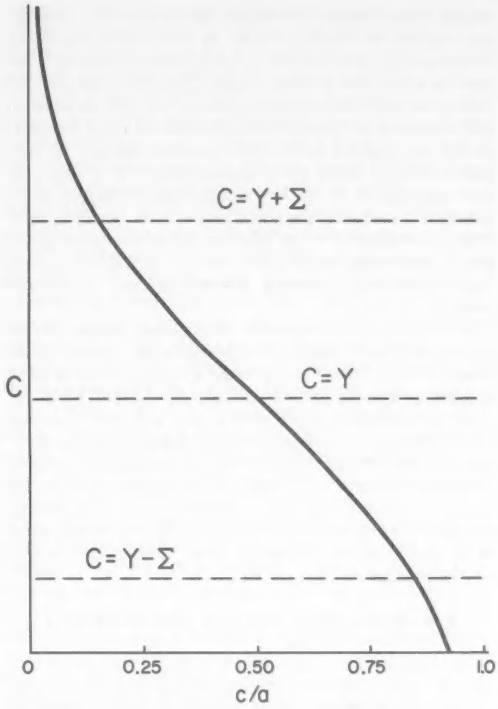

FIG. 2. Optimal capacity for fish processing as a function of c/a, where c is the cost of installing and maintaining the processing facilities and a is the net return.

pected to exceed the processing capacity roughly half the time. In this case the mean return is

$$\langle R\rangle_{\text{opt}} = (a - b - c)\,\bar{Y} - (a/\sqrt{2\pi})\,\Sigma$$
$$= (a/2 - b)\,\bar{Y} - (a/\sqrt{2\pi})\Sigma.$$

Combined Fishery Model

So far we have seen how the biological submodel predicts the mean and variance of the yield for various levels of exploitation, while the economic submodel shows how the processing capacity of the industry can be optimized to yield the largest mean return, given the mean yield and its variance. The system is assumed to be managed on the basis of a quota determined by the target value of the spawning stock; the management strategy, therefore, is based entirely on biological control of the resource. The purpose of combining these into a bioeconomic model is to use this biological control to maximize the return to the fishery. In the present case this is straightforward; the maximum mean return is a known function of $\bar{Y}$ and Σ^2, and these in turn depend on the control variable $\bar{P}$, so $\langle R\rangle_{\text{opt}}$ can be expressed as a function of $\bar{P}$ and maximized with respect to it. For the special case $c/a = 1/2$, this can be done in a simpler and more transparent fashion by finding the point where the Σ^2 vs. $\bar{Y}$ curve shown in

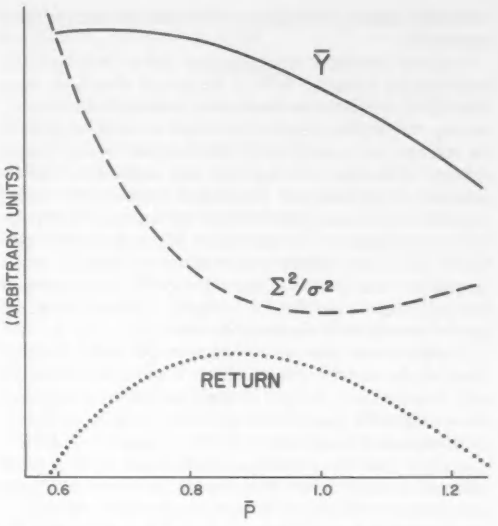

FIG. 3. Yield, variance, and return to the industry as a function of mean spawning stock size $\bar{P}$.

Fig. 1 is tangent to one of the straight lines along which $\langle R\rangle_{\text{opt}}$ is constant; if we set $b = 0$ the slopes of these lines are $\sqrt{\pi/2}$, and this tangent is shown in Fig. 1 for the case $\sigma^2 = 1$. A plot of $\langle R\rangle_{\text{opt}}$ vs. $\bar{P}$ is shown in Fig. 3 for these parameter values. From it we see that the optimum management strategy in this case is to try to maintain the stock at a level about 30% larger than that required for MSY, which reduces the mean yield by a little over 5% from the MSY level, but which reduces the variance of the yield by 45%. If we assume instead that $b > 0$, then the slope of the tangent line is correspondingly reduced, and the optimum parent stock level $\bar{P}$ approaches a limiting value 50% larger than the MSY level in the limit $b \to a/2$; the mean yield is correspondingly reduced by up to 13%, and the variance by a factor of 2. This is qualitatively reasonable, because b represents the amount that the processor loses on excess catch, and the larger b is, the more important it becomes to reduce the variance of the yield.

Alternate Model Formulations

The above calculations are specific to the particular model structure and parameter values used in the calculation. It seems unlikely that any single model could correctly balance all the social, economic, biological, and political factors affecting fisheries with sufficient generality to be applicable to all of them. On the contrary, it may be that each bioeconomic model of a fishery will prove unique in both quantitative and qualitative respects. Despite this complication, we can identify and classify several types of changes in model formulation which may aid in the application of these ideas to real fishery management problems. In order of increasing complexity, we can identify three classes of extension of the model presented above: alternate submodel structures, struc-

tures with additional linkages, and models that include more submodels.

Alternate submodel structures may derive from basically mathematical changes, such as the use of something other than a Ricker recruitment function in the biological submodel, or they may reflect significant changes in model dynamics; the constancy of a and b in the above model implies infinite elasticity of demand and supply for fish, and a more realistic submodel would make a a function of S and b a function of Y. However, because these changes are internal to the separate submodels, only the specialists concerned with a particular submodel need be concerned about them; it is not necessary for economists to know that the Ricker recruitment function is used, nor for the biologists to know about the detailed treatment of consumer demand.

Changes in the linkages between models are more profound. In the model developed above, it was assumed that the only information exchanged between the biological and economic submodels concerns the probability distribution for the yield, expressed in terms of its mean and variance. However, it is likely that the economists would want more detailed information, such as the size distribution of the catch. To provide this would require the use of age-structured models, and the biologists would in turn require information about the gear types and mesh sizes used in the fishery. Because these factors in turn have economic ramifications, there is a tendency for the demands for information to grow dramatically. This may lead to a situation where the submodels become impractically complex because of all the extraneous information they have to provide, and this can lead to submodels that produce numerical values containing very little real information. It is not unknown at present for managers to require estimates from scientists regardless of whether or not the scientists are capable of providing meaningful numerical values. Therefore it is important that the linkages between submodels be carefully worked out on a cooperative basis. It is not feasible work for one group to specify the necessary linkages for their submodel without consultation with the other modelers who are affected.

More complex still is the inclusion of additional submodels with all of their required linkages. The model described above has only two submodels, a biological model of the fish population dynamics and an economic model of the processing industry. One could include a submodel of primary fishing, of marketing and distribution, of national nutrition, and so forth. One could also couple this model, which originated as a single-species model, to others of the same type to build a multispecies fishery model. The extent to which this confounds the modeling process depends on how narrowly the interactions can be localized. For example, if the above economic submodel were generalized to include elasticity of demand for fish products, and if this elasticity were calculated by coupling to a marketing submodel, it would not affect the biological submodel. However, if the marketing submodel showed that parasites were a major factor affecting fish sales, then the biologists might be required to include this factor as a direct linkage to marketing.

Besides these three levels of increased elaboration of the model described here, there are different possible approaches to the optimization, implementation, and utilization of an interdisciplinary fisheries model. Equilibrium or steady-state models do not provide a realistic basis for fisheries management unless the fishery is close to the equilibrium levels. Otherwise, the cost of reaching the optimal equilibrium levels must be taken into account (Clark 1976). For example, if a fishery has been heavily overexploited, it might seem desirable to suspend all fishing for several years to allow the stocks to recover, but the social and economic impacts of such drastic strategy could prove unacceptable. As a more concrete example, it is widely conceded that improved quality standards would help the Canadian Atlantic fisheries; however, major changes in fish handling and processing practices would incur large initial costs, while it would take several years before the economic benefits reached satisfactory levels.

The construction of adequate bioeconomic fishery models is a major project which probably has to be repeated in the context of each fishery. In each case it is necessary to achieve a judicious balance between transparent simplicity and obscure but realistic complexity; it is also necessary to choose between the traditional equilibrium approach to fisheries management and the more realistic but mathematically complex techniques required to optimize a dynamical bioeconomic system over time (Clark 1976). The foregoing discussion does not provide a blueprint for such modeling, but it may show some general guidelines along which bioeconomic models may be organized.

The Skeena River Sockeye Salmon Fishery

The Skeena River fishery for sockeye salmon (*Oncorhynchus nerka*) provides a good case study of how economic considerations could be used to evaluate the trade-off between mean yield and variance in a real fishery. The number of returning fish is highly unpredictable, and Allen (1973) has shown that the ratio of returns to escapement is lognormally distributed, with ~20% of the measured ratios of returns to escapement differing from the mean value of 2.3 by a factor greater than two. The actual catches in this fishery have ranged from a few hundred thousand fish to over 2 million fish, so variable supply is clearly a problem. A constant escapement policy should produce close to the maximum possible mean yield, but because returns are a random function of escapement, the catches under this policy would be quite variable. The variance can be minimized by implementing a constant catch quota, but this would have to be set at a value well below the maximum mean yield to avoid decimating the stock in a series of bad years. A comprehensive set of strategies has been evaluated for this fishery by Walters (1975). He shows that the variance–mean yield relationship is similar to the solid part of the curve in Fig. 1, and that each possible strategy represents a different trade-off between yield and variability.

Walters (1975) did not construct an economic submodel to couple to his biological model of the yield and variance of the Skeena sockeye fishery; rather he assumed that the optimal balance between yield and variance could be achieved by minimizing the mean value of $(H - \mu)^2$, where H is the annual catch and μ is a parameter which can be adjusted to fit economic objectives. With this objective function he was able to use dynamic programming to arrive at optimal management strategies for each value of μ, and these strategies define the

"Pareto frontier" or trade-off curve for the fishery. Unfortunately, the parameter μ depends on biological as well as economic factors, because it is measured in "stock units" which depend on the position of the dome in the Ricker curve. Although Walters (1975), Allen (1973), and other researchers have postulated the existence of such a dome with maximum returns occurring for an escapement of from 1 to 2 million fish, the data do not provide strong evidence for this value; a linear regression of $\ln(R/E)$ against E gives a 95% confidence range of 0.3×10^{-6} to 1.2×10^{-6} for the slope, which corresponds to a location for the dome at an escapement which could be <900 000 fish or >3 000 000. It may in fact be that the optimal escapements and returns for this fishery are considerably larger than any in the historical record. This hypothesis cannot be tested unless escapements are greatly increased, but this would be an expensive experiment to undertake. One of the advantages of bioeconomic modeling is that it enables the costs and possible benefits of such management experiments to be translated directly into economic terms. This lessens the chance that the fishing industry will feel it is being asked to underwrite costly research programs that appear to be of interest only to the scientific community (Walters and Hilborn 1976; Silvert 1978).

The economic objectives described by the economic submodel I have described here cannot be expressed in terms of Walters' (1975) objective function, but this is unimportant, because the dynamic programming approach which he describes requires only that the economic objectives of the fishery be expressed in terms of a mathematical function to be maximized. Other considerations, such as the necessity of reserving part of the catch for the native fishery and equitable distribution of the remainder among various sectors of the fishing community, can be dealt with by techniques which have become an established part of the optimization literature.

It does not seem worthwhile to attempt to build a realistic economic submodel of the Skeena sockeye fishery at this point, because it is an economically and socially complex system which could only be dealt with adequately in a forum where all the different sectors of the fishery could be heard from and where political factors could be taken into account; this is generally the case and no doubt explains why biological models are so numerous and diverse relative to economic and social models. It is, however, interesting to note that if we use the economic submodel developed above with the parameter values $a = 2c$ and $b = 0$, then the optimal tangent line intersects the Pareto frontier at a point very close to what Walters refers to as "a simplified strategy for practical implementation," namely a catch rate which is zero for stock sizes less than 0.5 million fish, 50% for stocks larger than 1.0 million fish, and increases smoothly from 0 to 50% in between (cf. Fig. 8 of Walters 1975). This agreement may be purely fortuitous, but it could also reflect a basic robustness of bioeconomic management strategies. This can only be ascertained by studying the sensitivity of the optimal strategies to the assumptions and parameter values that are used to construct the models. In the case of the Skeena sockeye fishery it is not clear whether the best bioeconomic approach would be to couple a realistic economic submodel to the dynamic programming formalism of Walters' 1975 paper, or to pursue an active adaptive strategy of high escapements to find out whether economically beneficial increases in salmon returns would occur if escapements were greatly increased (Walters and Hilborn 1976; Silvert 1978).

Discussion

There are two main points in this paper. The first is that fisheries biologists should recognize the importance to the industry of providing more comprehensive descriptions of predicted fish supply than simply mean "sustainable" levels. I have focused on the importance of estimating the variance of future yields, but there are certainly other factors such as size distributions which are of commercial importance (some of this information is now made available, but usually on an informal basis). The second point is that detailed descriptions can be used to link biological and economic submodels of a fishery in such a way that the biological controls exercised by management can be evaluated in economic terms. This type of linkage is essential if systematic improvements in the fishing industry are to be achieved.

At the present time the management of most fisheries is fragmented to the extent that the interaction between different components of management has become virtually an adversary relationship (anyone who questions this is invited to look at the letters columns of Canadian Fishing Report, February and March 1981). The industry wants a good supply of fish, which leads to conflict with biologists who want to maintain large stock levels and keep recruitment high by restricting fishing; this puts them into the often maligned position of managing the fishery for the benefit of the fish. The marketing agencies in turn complain that they are getting poor quality products, and often they are unable to meet a demand for mature fish because these are too rare in a heavily exploited fishery. By defining a set of variables which are of common interest (e.g. mean yield, variance, size distribution, etc.) and designing submodels of the various sectors of the industry which use these variables as inputs and outputs, these submodels can be linked so that specialists involved in each sector can understand how their concerns are coupled to those of other individuals concerned with the fishery.

This approach is superficially similar to the well-known workshop methodology, where a small group of experts from various specialities spend some time building a master model and then spend the next few years complaining that it is not being used. I suggest instead that each active management group build and maintain its own submodel as an objective means of communicating its own concerns to other groups concerned with fisheries management. These submodels will change as management options and strategies change, and the linkage will never be perfect. It would be ideal if biologists, economists, sociologists, and everyone else associated with the fishing industry fully understood each other's work so that fisheries management could work towards a common goal in a common language and in a fully coordinated way. Until this happens it may be useful to realize that the formulation of submodels to quantify the thinking of each group creates a common language, and the linkage of these submodels provides an objective way to evaluate the industry-wide impacts of changes in the functioning of any particular subsystem.

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Factors Influencing Orthophosphate Turnover Times: a Comparison of Canadian and New Zealand Lakes

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WHITE, E., G. PAYNE, S. PICKMERE, AND F. R. PICK. 1982. Factors influencing orthophosphate turnover times: a comparison of Canadian and New Zealand lakes. Can. J. Fish. Aquat. Sci. 39: 469–474.

Fifty-five samples of lakewater from 21 New Zealand and 9 Canadian lakes were analyzed for dissolved phosphate, particulate phosphorus, and particulate nitrogen. The particulate N was used as an estimate of phytoplankton biomass and the ratio of particulate N to particulate P was used as an indicator of phosphorus sufficiency or deficiency within the biota. ^{32}P-PO_4-derived turnover times were found to be positively related to the size of the dissolved phosphate pool, negatively related to biomass, and were short where phosphorus deficiency existed. The amount of particulate nitrogen in the Canadian lake samples probably indicates an abundance of this nutrient in Canadian waters relative to that found in New Zealand. High seston N/P ratios in Canadian samples indicate a degree of phosphorus shortage in biota which is seen in few New Zealand waters.

Key words: orthophosphate, turnover times, particulate phosphorus, particulate nitrogen, plankton biomass, phosphorus deficiency, Canadian lakes, New Zealand lakes

WHITE, E., G. PAYNE, S. PICKMERE, AND F. R. PICK. 1982. Factors influencing orthophosphate turnover times: a comparison of Canadian and New Zealand lakes. Can. J. Fish. Aquat. Sci. 39: 469–474.

Cinquante-cinq échantillons d'eau de 21 lacs de la Nouvelle-Zélande et de 9 du Canada ont été analysés en vue d'y déterminer les teneurs en phosphate dissous, phosphore particulaire et azote particulaire. Ce dernier a servi à estimer la biomasse du phytoplancton, tandis que le rapport N particulaire à P particulaire a été utilisé comme indice de suffisance ou d'insuffisance de phosphore dans la biocénose. On a constaté que les temps de renouvellement dérivés de ^{32}P-PO_4 étaient en corrélation positive avec la masse de phosphate dissous, en corrélation négative avec la biomasse et que ce temps était court là où existait une déficience de phosphore. La quantité d'azote particulaire dans les échantillons des lacs canadiens indique probablement une plus grande abondance de cet élément nutritif dans les lacs canadiens que dans les lacs néo-zélandais. Les rapports élevés de N/P sestonique dans les échantillons canadiens sont le signe d'une insuffisance de phosphore dans la biocénose que l'on n'observe pas dans les eaux néo-zélandaises.

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THIS investigation describes the interacting influences on turnover times, of phosphate concentration, biomass, and phosphorus demand by biota. These interactions were examined in lake waters from three geographically distinct regions with the object of relating the biotic responses to what appear to be major differences in the relative abundance of nutrient nitrogen and phosphorus reaching lakes. This is of importance to management of eutrophication in New Zealand, where some lakes receive natural phosphorus loads of such magnitude that effective control by phosphorus load reduction appears impractical.

Almost all of the information was derived from samples collected from near-surface waters in summer, so that neither natural light nor temperature could be expected to restrict significantly phosphate uptake by plankton.

Turnover times for dissolved orthophosphate in lake waters are calculated by examining the rate at which carrier-free radioactive phosphate (^{32}P-PO_4) is removed from solution by plankton (Rigler 1956). When turnover times are short, they are attributed to shortage of dissolved phosphate in lake water or to an abundant phytoplankton (Rigler 1956, 1968; Lean

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TABLE 1. Regression equations (A–I) relating independent variables in several combinations to turnover times. The independent variables are dissolved phosphate (P-PO_4), particulate phosphorus (PP), and particulate nitrogen (PN) concentrations ($mg \cdot m^{-3}$), together with particulate nitrogen to phosphorus ratios (PN/PP). The dependent variable is ^{32}P-PO_4-derived turnover times (TT) (min). All data multiplied by 100 and transformed by $\log_{10}$.

	Equation			Independent variables							
				'P-PO_4'		PP		PN		PN/PP	
	r^2	df	P	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P
A	0.59	51	<0.0001	+0.840	<0.0001	+1.680	<0.0001	−2.377	<0.0001		
B	0.59	51	<0.0001	+0.843	<0.0001			−0.698	<0.001	−1.673	<0.001
C	0.59	51	<0.0001	+0.843	<0.0001	−0.699	<0.001			−2.370	<0.0001
D	0.51	52	<0.0001	+0.416	<0.05					−2.458	<0.0001
E	0.47	52	<0.0001			+2.868	<0.0001	−3.001	<0.0001		
F	0.46	53	<0.0001							−2.919	<0.0001
G	0.25	53	<0.001	+0.836	<0.001						
H	0.04	53	ns					−0.390	ns		
I	0.01	53	ns			+0.191	ns				

and Nalewajko 1976; Levine and Schindler 1980). Long turnover times are associated with abundant dissolved phosphate, scarcity of biota, or physical conditions inappropriate to growth (Peters 1975; Rigler 1964, 1966). Phosphorus sufficiency within plankton (Lean and Nalewajko 1979) or growth limitation caused by shortage of some other nutrient seems likely to be an additional reason for long turnover times.

The difficulties associated with obtaining satisfactory estimates of very low orthophosphate concentrations and the shortage of reliable and comparable biomass estimates have restricted examination of the way these factors influence turnover times to general statements.

We combined Sephadex gel chromatography with a very sensitive molybdenum blue method to estimate the concentration of low molecular weight reactive phosphorus (P-PO_4), which is as close to orthophosphate as has been possible to achieve so far with colorimetric methods.

Measurements of particulate phosphorus (PP) and particulate nitrogen (PN) were used as estimates of biomass. The seston N/P ratio was used as an indicator of phosphorus sufficiency or deficiency in biota.

Materials and Methods

Water sample collection, filtration, Sephadex gel chromatography, and associated analyses of low molecular weight phosphorus (P-PO_4), analyses of particulate phosphorus (PP), and the estimation of ^{32}P-PO_4 turnover times (TT) were carried out as described by White et al. (1981).

Particulate nitrogen (PN) analyses were carried out on the material collected for PP analyses, and the digestion procedure was the same. The ammonia–nitrogen produced was estimated colorimetrically by the method of Searle (1975).

The data set of 55 samples was that used by White et al. (1981), and includes waters from 9 lakes in Ontario, Canada, 7 Westland lakes in the South Island of New Zealand, and 14 lakes in the central volcanic plateau of the North Island of New Zealand.

Multiple regression analyses were used to examine factors affecting turnover times (Bailey 1959). The distribution of the TT was irregular, many being short and a fair number being long. Some statistical improvement in the TT frequency distribution was obtained by logarithmic transformation. Graphical representation was also improved. For these reasons parameters in the investigation were multiplied by 100 and transformed by $\log_{10}$. Testing for the difference between means for small groups of samples with potentially different variances followed the method of Bailey (1959).

The complete data set is available from the authors on request.

Results and Discussion

The result of a multiple regression using P-PO_4, PP, and PN concentrations as independent variables to describe the variability in TT is shown in line A of Table 1. The equation, which explained 59% of the variability in TT, was highly significant ($P < 0.001$). Each independent variable, in the presence of the other two, was highly significantly ($P < 0.001$) related to TT. The regression coefficients themselves are not readily interpretable because of the logarithmic transformation, but the positive or negative nature of the coefficients and their statistical significance is important. As expected, the TT increase as the P-PO_4 concentrations increase. TT shorten as PN increases, which is also interpretable; as biomass increases, turnover times are expected to decrease. However, TT also increase as PP increases, which is at variance with the TT versus PN coefficient if PP and PN both represent biomass. Of all coefficients of TT versus PP in Table 1, there is one other positive and significant relationship and that is where PP and PN are again jointly used as independent variables (line E). A positive but nonsignificant relationship occurs where PP is used as the only independent variable (line I). However, in the absence of PN as a variable, the relationship between TT and PP becomes highly significant ($P < 0.0001$) and negative (line C). It seems that in the absence of a better biomass estimate, PP assumes that role.

The regression coefficients relating PN to TT are all negative and highly significant ($P < 0.001$), except where PN is the only independent variable.

It is concluded that PN is a better indicator of biomass than PP. The explanation probably lies in the ability of phytoplankton to store substantial amounts of phosphorus as polyphosphates (Rhee 1973). Phosphorus can also be taken up in

quantity before the start of the growth which it stimulates (Lean and Nalewajko 1976; White and Payne 1980). Any circumstance which allows polyphosphate accumulation within the biota will cause PP to vastly overestimate biomass.

Introduction of the ratio PN/PP as an independent variable into the analyses provides an indicator of phosphorus sufficiency or deficiency within the phytoplankton. Wherever this parameter is used the regression coefficients with TT are negative and highly significant ($P < 0.001$) (Table 1, lines B, C, D, and F). Where phytoplankton are deficient in phosphorus, the TT are short. Even when PN/PP is the only independent variable, it explains 46% of the variability exhibited by the TT (Table 1, line F).

Wherever the P-PO_4 concentrations are included in the analysis, the relationship with TT is positive and usually highly significant ($P < 0.001$). Where P-PO_4 concentration is paired with PN/PP ratios as independent variables, the relationship between P-PO_4 and TT is marginally significant ($P < 0.05$) (Table 1, line D). Where P-PO_4 concentration is the only independent variable, the relationship with TT is positive and highly significant ($P < 0.001$) (Table 1, line G).

We concluded that phosphorus deficiency in phytoplankton is a major cause of short turnover times in the pool of dissolved phosphate. The size of that pool is also influential, as more phosphate leads to longer turnover times. However, its role is likely to be of secondary importance because of the speed with which phosphorus-deficient biota can adjust cellular N/P ratios in response to increase in orthophosphate concentration. Finally, the greater the biomass the shorter the turnover time is likely to be.

It would be satisfying to believe that the positive relationship between P-PO_4 concentration and TT indicates that our P-PO_4 estimates satisfactorily represent the true orthophosphate concentrations. This may not be so as the P-PO_4 estimates cover a substantial range (0.05−72 $mg \cdot m^{-3}$), and the high concentrations might largely dictate the slope and significance of the coefficient. To test this, we eliminated samples with P-PO_4 concentrations greater than 1.2 $mg \cdot m^{-3}$ from the data set, leaving 32 samples. This removed many of the longer turnover times (max. 10 000 min), but left some as long as 5670 min, and removed others as short as 2 min. A multiple regression using P-PO_4, PN, and PN/PP as independent variables for this reduced data set explained 44% of the variability in TT ($P < 0.001$), and the coefficients were similar to those in line B of Table 1, with a statistical significance of $P < 0.02$, $P < 0.05$, and $P < 0.01$, respectively. Thus a positive and significant relationship existed between TT and P-PO_4 when the range of P-PO_4 only extended from 0.05 to 1.2 $mg \cdot m^{-3}$, providing support for the view that the estimates are reasonably representative of orthophosphate in lake water, or of material readily converted to orthophosphate by phytoplankton and bacteria.

Although the three independent variables in the equations of lines A, B, and C (Table 1) are all highly significantly related to TT, 41% of the variability remains unexplained. This might be associated with inadequate reliability of the P-PO_4 estimates, which at low levels reach the limits of detection (White et al. 1982). In addition, the use of PN as an estimate of biomass is not totally satisfactory. The capacity of biota to store nitrogen to some extent (McCarthy and Goldman 1979) will lead to variable biomass estimates, and

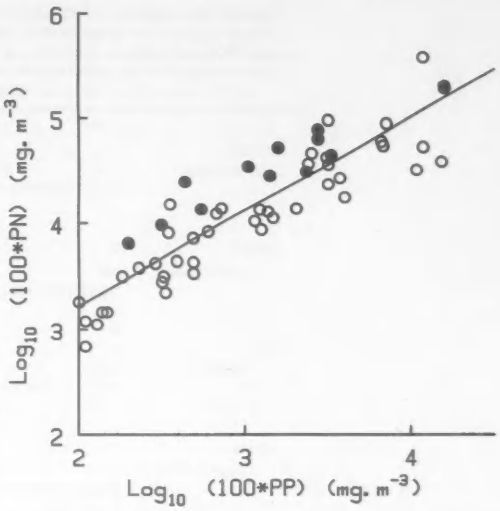

FIG. 1. Relationship between particulate nitrogen (PN) and particulate phosphorus (PP) in waters from some Canadian (●) and New Zealand (○) lakes.

periods of nitrogen sufficiency in the phytoplankton are likely to be associated with short turnover times, which will emphasize the negative relationship between TT and biomass. Detrital N present among the biotic N in variable proportion will inevitably reduce the usefulness of seston N as an indicator of biomass.

The relationship found between biomass and TT was unexpected, for recent findings of Lean (1982) show that short turnover times are largely dictated by bacteria and microalgae which are likely to form only a small part of the total PP and PN. More of the variability in TT might be explained if the biomass could be size-fractionated.

The relationship between PN and PP in our data is shown in Fig. 1. Of particular interest is the distribution of the Canadian lake samples relative to the mean. They span almost the entire range of PP values, but all points lie above the regression slope. The ratios for Canadian samples are substantially higher than for New Zealand samples; the statistical significance of the difference is confirmed in Table 2. The PN in the Canadian samples is on average higher ($P < 0.01$) than in those from New Zealand, whereas average PP content and average P-PO_4 concentration of the Canadian waters was not statistically different from the New Zealand samples.

The implication is that the biota in New Zealand waters are nitrogen deficient by comparison with biota in the Canadian samples. This is consistent with our view that the inorganic nitrogen content of New Zealand groundwaters, rivers, lakes, and rainfall is less than that generally found in Europe and North America (Vollenweider 1968). Under such circumstances nitrogen limitation to phytoplankton growth might occur more frequently in New Zealand. Evidence suggesting nitrogen limitation has been produced for Lake Taupo (White and Payne 1977) and Lake Rotorua (White and Payne 1978; Vincent 1982a). Figure 2 supports this, as the data from Lakes

TABLE 2. A comparison of Canadian and New Zealand lake water samples in terms of their dissolved phosphate (P-PO_4), particulate phosphorus (PP), particulate nitrogen (PN) concentrations, and ratios of particulate nitrogen to phosphorus (PN/PP).

		Canadian	New Zealand	*P.*
	n	12	43	
PN/PP	$\bar{x}$	26.96	12.71	
(Arithmetic)	var.	152.20	63.41	
	Mean difference 14.24 df 14			≤0.002
	n	12	43	
PN/PP	$\bar{x}$	3.39	3.03	
(Logarithmic)	var.	0.039	0.062	
	Mean difference 0.355 df 23			<0.0001
	n	12	43	
PN	$\bar{x}$	4.518	4.062	
(Logarithmic)	var.	0.169	0.411	
	Mean difference 0.456 df 28			<0.01
	n	12	43	
PP	$\bar{x}$	3.127	3.028	
(Logarithmic)	var.	0.277	0.438	
	Mean difference 0.099 df 22			ns
	n	12	43	
P-PO_4	$\bar{x}$	1.719	2.084	
(Logarithmic)	var.	0.299	0.546	
	Mean difference −0.365 df 23			ns

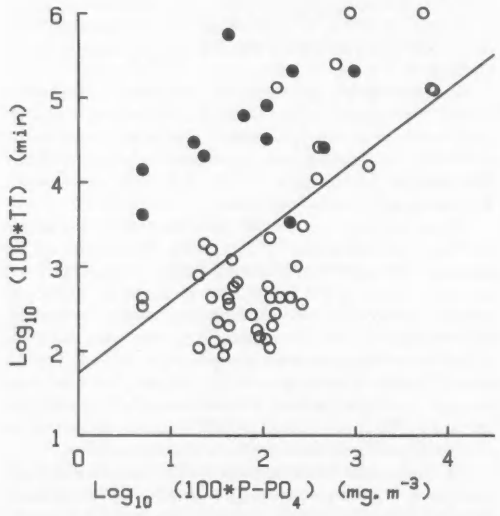

FIG. 2. Relationship between ^{32}P-PO_4-derived turnover times (TT) and dissolved phosphate (P-PO_4) concentrations, for samples from Lakes Taupo and Rotorua (●), and other New Zealand and Canadian lakes (○).

Taupo and Rotorua show much longer turnover times than expected on the basis of their 'P-PO_4' content.

The central volcanic plateau of the North Island of New Zealand is liberally coated with ash over some 26 000 km^2, and much of this gives up substantial amounts of phosphorus on leaching. Large-volume cold-water springs are common and frequently contain dissolved phosphate in high concentrations. The Hamurana Spring near Lake Rotorua has a mean flow of 3 $m^3 \cdot s^{-1}$ and contains phosphate−phosphorus at 81 $mg \cdot m^{-3}$ (Fish 1975). A spring feeding Lake Rotongaio, near Taupo, contains phosphate−phosphorus at 260 $mg \cdot m^{-3}$. A great many springs in the northeast quadrant of Lake Taupo's catchment discharge phosphorus at concentrations between 40 and 100 $mg \cdot m^{-3}$. White and Downes (1977) estimated the reactive phosphorus load on this lake to be enough to make it mesotrophic (Vollenweider 1976) although it is clearly oligotrophic (White et al. 1980).

By comparison the catchments of the Westland lakes in the South Island of New Zealand do not give up much phosphorus, and the nutrient nitrogen to phosphorus ratios available to biota are likely to be high. Paerl et al. (1979) considered the phytoplankton of these lakes to be phosphorus deficient.

The PN/PP ratios in our data ranged between 3 and 57. Much of this variability can be associated with the regional differences in nutrient supply described above. Table 3 shows this, with most of the groups being significantly different from one another. A gradation of ratios occurs in New Zealand lakes, with low values (average 8.61) occurring in two lakes where independent evidence (White and Payne 1977, 1978; Vincent 1982b) suggests that phytoplankton growth is limited by insufficient nitrogen. The phytoplankton from other lakes in the central volcanic plateau appears to be relatively phosphorus sufficient (with an average seston N/P

TABLE 3. The difference in nitrogen to phosphorus ratios (PN/PP) in the particulate material of Canadian and three groups of New Zealand lakes.

	Mean PN/PP	Significance of difference of NP/PP ratios between groups of lakes		
Rotorua and Taupo, North Island, N.Z.	8.61	$P<0.001$	$P<0.01$	$P<0.02$
Other North Island lakes in N.Z.	13.79	$P<0.01$	ns	
Westland lakes, South Island, N.Z.	16.06	$P<0.02$		
Ontario lakes, Canada	26.96			
		Ontario lakes, Canada	Westland lakes, N.Z.	Other North Island lakes in N.Z.

ratio of 13.79). The phytoplankton of the Westland lakes in the South Island of New Zealand has been described as phosphorus deficient, and this may be supported by seston N/P ratios which average 16.06. However, this mean ratio is still very much less than that from the Canadian samples (average 26.96). Phosphorus sufficiency in biota is apparent at one end of the series, while at the other end phosphorus deficiency is the rule.

The Ontario lakes in our investigation are well known limnologically (Rigler 1964, 1968; Lean 1973), and no reference has been made to peculiarities of either their phosphorus dynamics or their nitrogen status. They may well be representative of the Canadian lakes, yet they are demonstrably different from New Zealand lakes in characteristics which are directly related to the relative importance of nitrogen and phosphorus to biota.

We conclude that N/P ratios in seston can be used as indicators of sufficiency or deficiency of phosphorus in the plankton, and note that a general relationship exists between the seston ratios and the relative abundance of nutrient nitrogen and phosphorus reaching lakes.

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Planktivorous Feeding Ecology of Arctic Grayling (*Thymallus arcticus*)

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SCHMIDT, D., AND W. J. O'BRIEN. 1982. Planktivorous feeding ecology of Arctic grayling (*Thymallus arcticus*). Can. J. Fish. Aquat. Sci. 39: 475–482.

A component analysis approach was applied to studies of the zooplankton feeding of Arctic grayling (*Thymallus arcticus*) of 3–20 cm standard length using all arctic zooplankton species common in the area. Unlike other fish species, larger grayling have greater reactive distance. As expected, the ability of grayling to locate prey was found to increase with size of prey and with light intensity. Grayling vision was found to increase dramatically at light intensities higher than 100 lx. Generally, grayling located and attacked any species within the visual field, locating all by core body size. One exception was the copepod *Diaptomus pribilofensis*, which was of appropriate size and pigmented a bright red, but was never attacked and eaten by any grayling. The large copepod *Heterocope septentrionalis* was able to evade grayling feeding attack, but *Heterocope* evasion was dependent on grayling size and water temperature. Analysis of inter-gill-raker spacing showed that spacing increases linearly with fish length up to 13 cm, at which length no further increase was observed. Such change in inter-gill-raker spacing suggests the feeding niche of grayling may be broader than that of similar sized, temperate centrarchid planktivores.

Key words: Arctic grayling, *Thymallus arcticus*; planktivorous fish, predator–prey interaction, prey evasion, zooplankton

SCHMIDT, D., AND W. J. O'BRIEN. 1982. Planktivorous feeding ecology of Arctic grayling (*Thymallus arcticus*). Can. J. Fish. Aquat. Sci. 39: 475–482.

Une analyse des composantes a été appliquée à des études d'alimentation zooplanctonique d'ombres arctiques (*Thymallus arcticus*) de 3–20 cm de longueur standard, entièrement nourries d'espèces zooplanctoniques arctiques communes dans la région. Contrairement aux autres espèces de poissons, les grands ombres ont une distance de réaction plus grande. Comme on s'y attendait, on constate que l'aptitude des ombres à localiser une proie augmente en fonction de la taille de cette dernière et de l'intensité lumineuse. La vision chez les ombres augmente de façon dramatique à des intensités lumineuses dépassant 100 lx. Les ombres localisent et attaquent généralement toute espèce qui se trouve dans leur champ de vision, les localisant toutes d'après la taille du centre de leur corps. Le copépode *Diaptomus pribilofensis*, est toutefois une exception : malgré une taille appropriée et un corps pigmenté d'un rouge brillant, il n'est jamais attaqué et mangé par un ombre. Le grand copépode *Heterocope septentrionalis* peut éviter l'attaque des ombres, mais l'évasion de ce copépode dépend de la taille de l'ombre et de la température de l'eau. Une analyse de l'espace séparant les branchicténies démontrent que cet espace augmente en fonction linéaire de la longueur du poisson jusqu'à 13 cm et que, passé cette longueur, il n'y a plus d'autre augmentation. Un tel changement de l'espacement des branchicténies donne à croire que la niche alimentaire de l'ombre peut être plus étendue que celle de centrarchidés planctivores tempérés de même taille.

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IVLEV (1955) was the first ecologist to begin systematic study of what prey a predator would consume. He pointed out two important components that may alter the feeding pattern: the accessibility of the prey and the preference of the predator. Holling (1959), and later Gerritsen and Strickler (1977) and O'Brien and Vinyard (1978), described the act of predation as a series of discrete components, each of which may alter the diet composition. In this analysis, each predation cycle is divided into the following sequential events: location, pursuit, attack, and capture. Each event is independent and can be analyzed and quantified experimentally and then combined

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for a composite picture of the mechanisms behind the feeding ecology of a species (O'Brien 1979).

In this paper we present such an analysis for Arctic grayling (*Thymallus arcticus*). Arctic grayling is a cold-water species widespread throughout arctic and subarctic North America, and smaller individuals are commonly planktivorous. Grayling are the major planktivores in the Toolik Lake region of Alaska (68°37′N, 145°35′W) where these studies were performed. Toolik Lake is ~ 200 km south of Prudhoe Bay along the Alaska oil pipeline haul road.

Methods

The Arctic grayling used in these experiments ranged in size from 3 to 20 cm and were collected by dipnetting, seining, and angling. The fish were maintained in several 120 × 30 × 30 cm Plexiglas aquaria in an unheated laboratory building at the Toolik Lake Camp. The fish were fed daily with pond and lake zooplankton, and all remained active and fed throughout the experimental period.

Zooplankton used in these experiments were collected from two lakes with fish (Toolik Lake and Lake N2) and two nearby fishless ponds. *Daphnia pulex* and darkly pigmented *Heterocope septentrionalis* were collected from the ponds, and *Daphnia longiremis* f. *typica* (Riessen and O'Brien 1980) was collected from Lake N2. All other zooplankton used, *Daphnia longiremis* f. *cephala*, *Bosmina longirostris*, *Cyclops scutifer*, and lightly pigmented *H. septentrionalis*, were collected from Toolik Lake. Most experiments were performed shortly after collection of the zooplankton; however, the *Heterocope* evasion experiments required a temperature acclimation period for the fish and copepods.

Locating the Prey

We conducted forward-directed, reactive-distance experiments by placing one fish in a holding aquarium modified by the addition of an opaque Plexiglas corridor placed in the aquarium to restrict the lateral movement of the fish and assure that a forward-directed reactive distance was always measured. The corridor was always wide enough that the fish could turn around easily. To make reactive-distance measurements, we used an eye dropper to place a single prey in the corridor while a fish was swimming toward the opposite end of the aquarium. The reactive distance was considered to be that point at which the fish, after turning and beginning to cruise towards the prey, clearly focused on the prey and accelerated; following this the fish always swam directly up to and consumed the prey. Measurements were taken with all the arctic zooplankton species common in the Toolik area (O'Brien et al. 1979), using individuals of various sizes, four light intensities, and four different sizes of fish.

Zooplankton prey were sized with a Wild M-5 dissecting microscope with an ocular micrometer. *Daphnia pulex* and *B. longirostris* were measured from the tip of the head to the posterior of the carapace. *Daphnia longiremis* f. *cephala* and *D. l.* f. *typica* were measured from the compound eye to the posterior of the carapace. Body lengths of *C. scutifer* and *H. septentrionalis* were taken from the anterior of the cephalothorax to the anterior of the urosome as suggested by Kettle and O'Brien (1978).

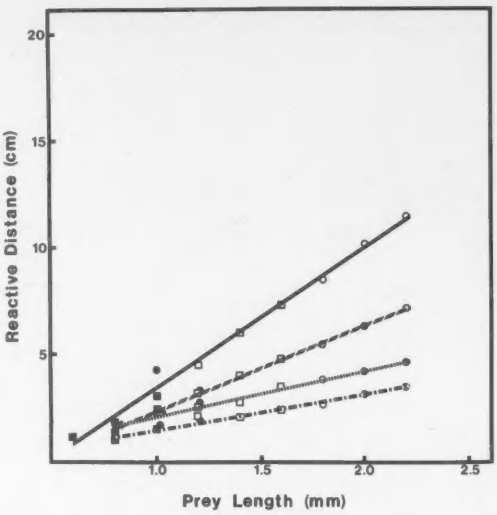

FIG. 1. Reactive distances of a 3-cm grayling at four light intensities with various sizes and species of zooplankton. (The solid line represents 1354 lx, the diagonally broken line represents 748 lx, the dotted line represents 48 lx, and the unevenly broken line is for 4.8 lx.) Open circles are the mean observations of *H. septentrionalis*, open squares are *D. longiremis*, solid circles are *C. scutifer*, and solid squares are *B. longirostris*.

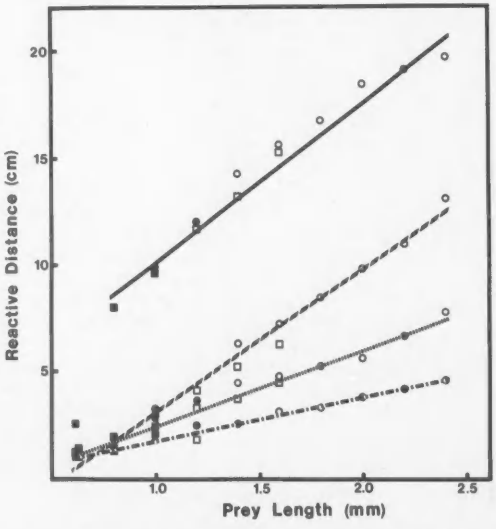

FIG. 2. Reactive distances of a 5.5-cm grayling at four light intensities with various sizes and species of zooplankton. (The solid line represents 1354 lx, the diagonally broken line is 748 lx, the dotted line is 48 lx, and the unevenly broken line is 4.8 lx.) Open circles are the mean observations of *H. septentrionalis*, open squares are *D. longiremis*, closed circles are *C. scutifer*, and closed squares are *B. longirostris*.

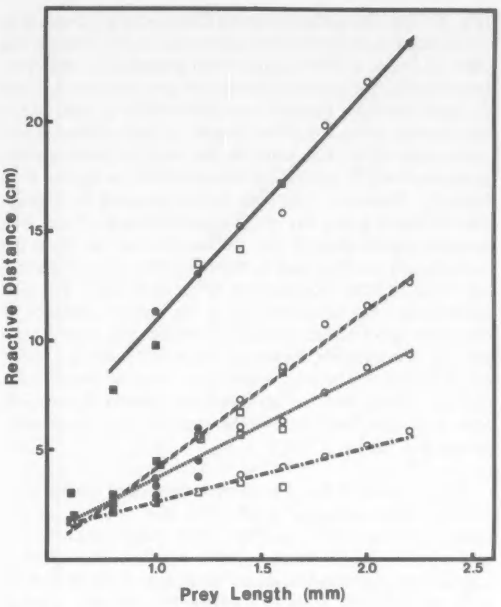

FIG. 3. Reactive distances of an 8.5-cm grayling at four light intensities with various sizes and species of zooplankton. (The solid line represents 1354 lx, the diagonally broken line is 748 lx, the dotted line is 48 lx, and the unevenly broken line is 4.8 lx.) Open circles are mean observations of *H. septentrionalis*, open squares are *D. longiremis*, closed circles are *C. scutifer*, and closed squares are *B. longirostris*.

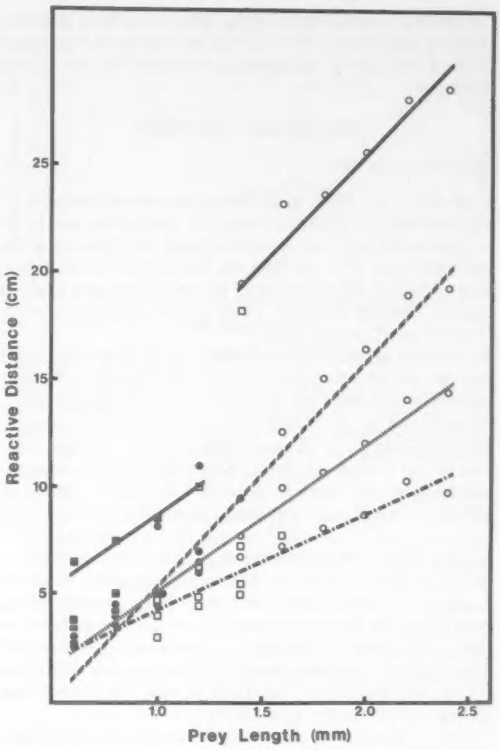

FIG. 4. Reactive distances of a 13-cm grayling at four light intensities with various sizes and species of zooplankton. (The solid line represents 1354 lx, the diagonally broken line is 748 lx, the dotted line is 48 lx, and the unevenly broken line is 4.8 lx.) Open circles are the mean observations of *H. septentrionalis*, open squares are *D. longiremis*, closed circles are *C. scutifer*, and closed squares are *B. longirostris*.

The location ability of grayling was investigated at four light intensities: 4.8, 48, 748, and 1354 lx. All but the highest light intensity were created with fluorescent lights either bare or wrapped in layers of plastic window screen to act as neutral density filters. The highest light intensity was achieved with sky light but not direct sunlight. After the field season it became apparent that information on the reactive distance at near full sunlight would be helpful. Although no direct measurements were made, we had filmed a 9.5-cm and a 13-cm fish feeding on 2-mm *Heterocope* in full sunlight (~20 000 lx) at 16:00 on August 15. On these films the reaction to the prey is quite apparent and the reactive distance can be accurately estimated using the known length of the fish as a scale factor.

To estimate the shape of the volume actually searched by arctic grayling, we measured the reactive distance of prey placed at right angles to the fish (side-directed reactive distance). These measurements were taken in a 91 × 46 × 15 cm Plexiglas aquarium fitted with an opaque partition dividing one-third of the aquarium. The partition was flared and had an opening through which the fish was conditioned to cruise back and forth. When the fish was inside the partition, prey could be positioned at various angles to the opening. Close observation of the fish as it swam through the opening allowed us to note the reactive distance. Data were obtained at several angles, but only those at right angles are included. Lake *Heterocope* were used with both 5.5- and 8.5-cm fish and a light intensity of 1354 lx.

PREY EVASION AND ESCAPE

We also estimated the evasion success of *Heterocope septentrionalis*, the only prey species tested able to evade grayling attack, at three different temperatures (5, 10, and 15°C). Fish of 3.0, 5.5, 8.5, and 13 cm standard length, along with a group of *Heterocope*, were acclimated to the test temperature for 24 h. An adult *Heterocope* was then introduced into the aquarium and the number of attacks necessary for successful capture were counted.

The likelihood of an individual zooplankter's escaping ingestion once taken into the buccal cavity is a function of the retention ability of the gill rakers (Drenner 1977). The cumulative gill-raker spacing was measured on 13 fish, ranging in standard length from 3.0 to 20 cm, by dissecting out the gill arches and measuring inter-gill-raker spacing and gill-raker height. The cumulative gill-raker spacing is the percentage

of specific inter-gill-raker space area to the total gill-raker filtering area (Boyd 1976). Actual measurements were made with a Wild M-5 dissecting microscope to the nearest 0.04 mm.

Results and Discussion

Locating the Prey

Fish size — Unlike other fish species whose feeding ecology has been investigated, in grayling the reactive distance to a given sized prey was found to change with the size of the grayling (Fig. 1–4). In only the largest fish at the highest light intensity did the reactive distances approach those of sunfish (Werner and Hall 1974; Confer and Blades 1975; Vinyard and O'Brien 1976).

No other group of fish has been shown to have increased reactive distance as they increase in size; frequently, however, fish of different sizes have not been tested. Wright (1980) showed that 8- to 16-cm crappie have identical reactive distances, and G. L. Vinyard (Department of Biology, University of Nevada at Reno, Reno, NV 89507, personal communication) reports no difference in reactive distance in different sized bluegill sunfish (*Lepomis macrochirus*).

Prey size — The forward-directed reactive distance of Arctic grayling to different lake species and sizes of prey at various light intensities increased linearly with increasing prey core body length in almost all cases (Fig. 1–4, Table 1). This is similar to earlier findings with sunfish (Werner and Hall 1974; Confer and Blades 1975; Vinyard and O'Brien 1976) and lake trout (*Salvelinus namaycush*) (Kettle and O'Brien 1978; Confer et al. 1978).

An exception to the strict linear increase in reactive distance with increasing prey size occurred at high light intensities in the three larger size-classes of fish. In this situation, reactive distance of the 13-cm-long fish decreased linearly with decreasing prey size down to prey 1.4 mm in length, where there was a clear discontinuity in the linear decline (Fig. 4). The extrapolated reactive distance for a 1.2-mm prey would be 17.5 cm whereas the measured reactive distance was only 10.2 cm, a 40% decline from expected to observed. Interestingly, the reactive distance for prey between 1.2 and 0.6 mm decreased linearly at a slope similar to that for the zooplankton above 1.4 mm in length. A similar although less pronounced effect was noted in the reactive distance measurements for 5.5- and 8.5-cm fish studied at the highest light intensity. However, with both fish of this size the discontinuity came at a prey size of 0.8 mm rather than 1.2 mm. The potential significance of this shift in the size at which the discontinuity occurred may be related to the ability of various sized fish to retain zooplankton by the gill rakers. No such discontinuity has been reported in the reactive distance of other fish species; the mechanism behind this change with grayling is not known. However, Ware (1973) found a curvilinear relationship between small bits of meat of various sizes and reactive distance of trout and the greatest discrepancy from a straight line was with the smallest prey item tested, around 2.3 mm.

Prey pigmentation — The reactive distance of similar sized fish to highly pigmented pond forms such as *D. pulex* and pond *Heterocope* was somewhat greater than for similar sized lake zooplankton at similar light intensities. The effect of zooplankton pigmentation is shown in Fig. 5 for an 8.5-cm fish, and the linear regression parameters for other sizes of fish are included in Table 1. The effect of prey pigmentation was especially notable with the larger fish tested and at high light intensities, whereas at 4.8 and 48 lx there was almost no difference between reactive distance of pigmented and nonpigmented prey of similar body size. Although at high light intensities reactive distances to pigmented prey were always greater than reactive distances to nonpigmented prey of similar length, the difference is not statistically significant. Lake trout were reported to show a more pronounced response to pigmentation of prey by Kettle and O'Brien (1978) and Confer et al. (1978).

Table 1. Slope, *y*-intercept, and square of correlation coefficient for the four sizes of fish and four light intensities used. The number of fish used for each regression is given. The left half of the table gives statistics for pond species of zooplankton and the right half for lake species.

Fish size	Light intensity (lx)	Pond				Lake			
		4.8	48	748	1354	4.8	48	748	1354
3.0 cm	Slope	20.3	26.6	45.2	63.4	16.4	22.0	40.2	65.5
	Intercept	−8.65	−11.0	−22.2	−11.0	−1.84	−1.47	−16.9	−30.9
	r^2	0.76	0.80	0.8	20.90	0.69	0.82	0.90	0.96
	No. fish	$n = 4$	$n = 4$	$n = 3$	$n = 5$	$n = 7$	$n = 9$	$n = 7$	$n = 11$
5.5 cm	Slope	22.2	32.5	68.2	82.3	20.8	34.2	67.7	76.6
	Intercept	−1.96	−4.42	−29.0	33.6	−3.51	−8.68	−37.0	25.0
	r^2	0.68	0.65	0.85	0.85	0.82	0.89	0.94	0.93
	No. fish	$n = 3$	$n = 3$	$n = 5$	$n = 7$	$n = 6$	$n = 6$	$n = 5$	$n = 10$
8.5 cm	Slope	30.4	49.3	91.4	109.8	24.7	47.9	72.9	110.3
	Intercept	−10.2	−16.8	−54.9	13.7	1.91	−10.5	−31.0	−4.91
	r^2	0.74	0.88	0.88	0.90	0.73	0.88	0.90	0.92
	No. fish	$n = 2$	$n = 2$	$n = 2$	$n = 4$	$n = 4$	$n = 4$	$n = 6$	$n = 7$
13.0 cm	Slope	71.4	78.8	48.2	92.5	44.2	67.9	106.7	110.3
	Intercept	−60.8	−37.4	93.3	88.0	−0.49	−14.5	−53.8	32.3
	r^2	0.95	0.95	0.66	0.85	0.83	0.94	0.87	0.68
	No. fish	$n = 3$	$n = 3$	$n = 2$	$n = 3$	$n = 5$	$n = 5$	$n = 5$	$n = 7$

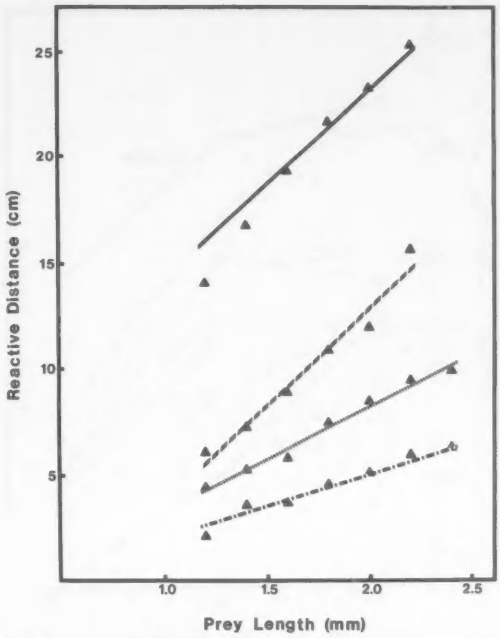

FIG. 5. Reactive distances of an 8.5-cm grayling at four light intensities with naturally pigmented pond *D. pulex* represented by the solid triangles. (The solid line represents 1354 lx, the diagonally broken line is 748 lx, the dotted line is 48 lx, and the unevenly broken line is 4.8 lx.)

Light intensity — As expected, the reactive distance of grayling was found to increase with increasing light intensity. Other species tested (bluegill sunfish, Vinyard and O'Brien 1976; white crappie (*Pomoxis annularis*), Wright et al. 1980; Wright 1981; and several salmonid species, Kettle and O'Brien 1978; Confer et al. 1978) appear to reach their maximum visual acuity at a light intensity of about 100 lx; brighter light appears to have little additional effect on location abilities.

In arctic grayling, we found reactive distance to increase up to a light intensity of 20 000 lx. Even in such intense light, grayling visual acuity barely approached that of other planktivorous species measured at less than 100 lx. Figure 6 shows the reactive distance of a 8.5-cm grayling to a 2-mm prey and a 13-cm grayling to a 1-mm prey at various light intensities. In both cases the reactive distance increased moderately with light up to 748 lx, above which point there is a marked increase in the reactive distance to the 2-mm prey but a lessened increase for the 1-mm prey.

This phenomenon has not previously been observed in a planktivorous fish species. Confer et al. (1978) found no increase in reactive distance with increasing light intensity above 50–100 lx with lake trout and brook trout (*Salvelinus fontinalis*). The results of Kettle and O'Brien (1978) working with lake trout at light intensities between 800 and 1200 lx are in substantial agreement with Confer's work. Thus, it appears that arctic grayling are unusual in their continuing increase in reactive distance with increasing light intensity.

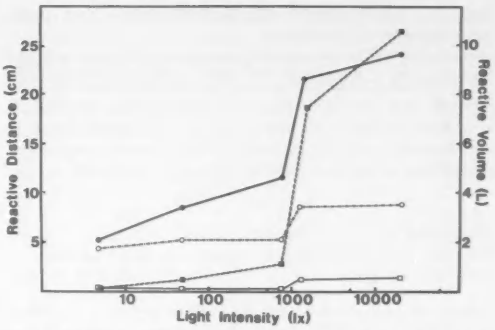

FIG. 6. Reactive distances and reactive volumes as a function of light intensity. The solid line represents the reactive distance of a 8.5-cm grayling to a 2-mm prey; the diagonally broken line represents the reactive volume of an 8.5-cm grayling to a 2-mm prey; the dot-dashed line represents the reactive distance of a 13-cm grayling to a 1-mm prey; and the dotted broken line represents the reactive volume of a 13-cm grayling to a 1-mm prey.

Only at light intensities higher than 1300 lx was the reactive distance of Arctic grayling similar to that of several sunfish at 50 lx. Because grayling, at least in the Arctic, may do much of their feeding under conditions of continuous daylight and very clear water, selection for low light vision may be low. Temperate fish, because they do much of their feeding during crepuscular periods, may be more highly adapted for low light situations.

Reactive volume — To determine the probability of grayling locating a given size of prey, it is important to determine the actual volume being searched by the fish. We therefore gathered preliminary data on side-directed reactive distances to get some estimate of the radius of the volume being searched by the fish. With both sizes of fish tested (5.5 and 8.5 cm), a prey placed to the side was significantly less likely to be located (Table 2). In all cases the reduction in reactive distance was very close to 60%. Thus we used this scaling percentage in computing the reactive volume for light intensities, prey sizes and species, and sizes of fish not actually tested in the side-directed reactive distance experiments.

The side-directed reactive distances increased in proportion with increasing fish size (Table 2), indicating that larger Arctic grayling can search much larger volumes of water than small ones. For example, a 5.5-cm grayling had a forward-directed reactive distance of 17.5 cm to a 2.0-mm lake prey at 1354 lx and a side-directed reactive distance of 10.3 cm to a similar sized prey under identical conditions. Assuming an ellipsoid of formula $V = a^2b^4/3$ where a is the side-directed reactive distance and b the forward-directed reactive distance, then a stationary fish can search a 3.89-L forward-directed ellipsoid. Using the measurements for the 8.5-cm fish, the reactive volume would be 7.38 L. No side-directed reactive-distance measurements were made for the 13- and 3.0-cm fish, but assuming the same relationship, their reactive volumes would be 12.3 and 0.75 L, respectively. Thus, a 13-cm fish would have a reactive volume more than 16 times larger than that of a 3.0-cm fish. Quite clearly, larger Arctic grayling

TABLE 2. Side-directed reactive distances for two sizes of fish using five sizes of *Heterocope*.

Fish size (cm)	Heterocope size (mm)	Reactive distance (mm)
5.5	1.6	70, 80, 100
5.5	1.8	85, 100, 105
5.5	2.0	95, 110
5.5	2.2	110, 125
5.5	2.4	110, 120
8.5	1.6	90, 100
8.5	1.8	110, 115
8.5	2.0	115, 140
8.5	2.2	140, 160
8.5	2.4	155

have the visual acuity to be more efficient planktivores. This might be expected as larger fish have greater retinal area (O'Connell 1963; Hester 1968) as well as greater overall energy needs.

Although having the best vision, large grayling are much less planktivorous than small grayling. Large grayling tend to feed on benthic or emergent insects (O'Brien et al. 1979), and in the present study, grayling larger than 17 cm could not, under any circumstances, be enticed to feed on lake zooplankton in the laboratory.

Grayling preference — Grayling tended to locate all lake prey equally on the basis of core body size, with some ability to locate pigmented pond *D. pulex* and pond *Heterocope* at slightly greater distances at high light intensities. The one dramatic exception to the grayling's catholic diet was its failure to attack *Diaptomus pribilofensis*. These copepods are ubiquitous in the lakes and ponds of the Toolik area, are colored a deep red, and range in size from 0.8 to 1.0 mm, similar to small *D. pulex*, which was readily located and eaten Yet no matter how close grayling came to *D. pribilofensis*, they never attempted to attack them.

Drenner et al. (1978) demonstrated that freshwater calanoid copepods can frequently evade a simulated fish suction intake, and Kettle and O'Brien (1978) showed that *D. pribilofensis* at 15°C could evade a small lake trout suction intake 40% of the time. Thus, the failure to attack *D. pribilofensis* may be related to the prey's ability to evade capture. Vinyard (1980) showed that sunfish would learn which of two artificially colored *Daphnia* was made to evade and attack the other color. It seems strange, however, that even starved grayling did not even attempt to attack *D. pribilofensis*. In any event, such a marked lack of interest by the dominant planktivore in these lakes explains the maintenance of the red pigmentation which doubtless increases visibility to predators but may decrease mortality under conditions of bright light (Hairston 1979; Luecke and O'Brien 1981).

PREY EVASION AND ESCAPE

Grayling of all sizes could capture all tested cladocerans 100% of the time. With *Heterocope*, the capture success varied considerably (Fig. 7). Graylings' ability to capture *Heterocope* increased with size of fish up to the 8.5-cm fish. The poor capture ability of the smaller fish (3.0 cm) is probably due simply to small buccal volume and thus reduced

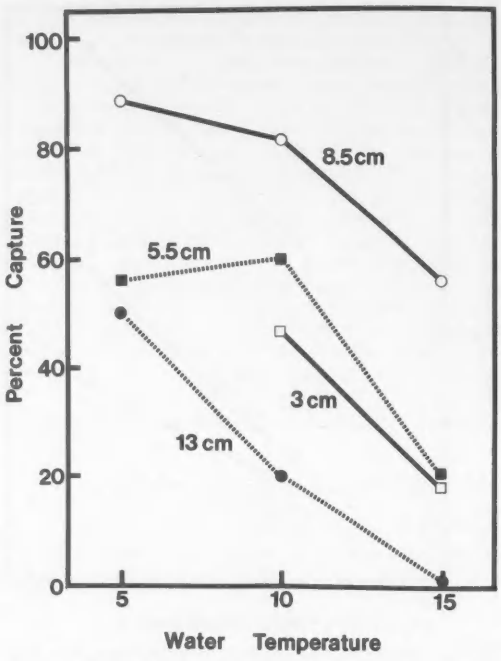

FIG. 7. Capture success as a function of water temperature for four sizes of grayling attempting to capture adult *H. septentrionalis*. The sizes of grayling used are listed on the graph.

sustained suction. However, the largest fish tested (13 cm) had the lowest *Heterocope* capture success, possibly because of a general lack of interest in zooplankton as food. The 13-cm grayling was about the largest we found to feed on zooplankton under laboratory conditions; larger fish (17.0 cm) never attacked zooplankton but avidly ate adult mosquitoes hovering just above the aquarium water surface.

The common observation that fish tend to feed more heavily on copepods in winter than in summer (Eggars 1978) suggested a relationship between water temperature and capture success. We therefore studied grayling predation on *Heterocope* at three temperatures and found that capture success decreased, the warmer the water (Fig. 7). This result can be attributed to the fact that grayling swimming speed and behavior are hardly affected by a change from 5 to 15°C, whereas *Heterocope* move much more slowly in colder water.

Once captured, zooplankton prey can escape only by slipping through the fish's gill rakers. Our measurements of grayling gill-raker spacing indicated the larger fish were able to retain about half those food items whose smallest dimension was 0.5 mm or smaller (Fig. 8). In some preliminary measurements we found that for both cladocerans and copepods the smallest body dimension was not length but one aspect of body width and was generally fully two-thirds smaller than body length. Only rough estimates of size of prey retained can be made because of the uncertainty of the position and firmness of various antennae and other protruding structures of

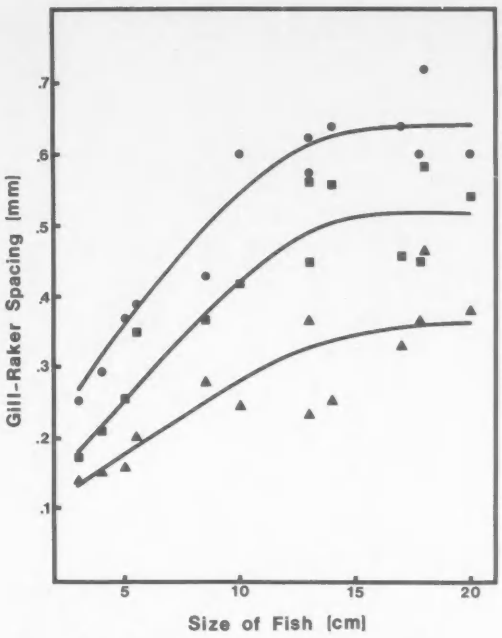

FIG. 8. Cumulative gill-raker spacings as a function of fish size. The uppermost line is a curvilinear plot through the solid circles representing 95% capture efficiency of the gill rakers. The middle line through the solid squares represents 50% capture efficiency. The lower line through the solid triangles represents 5% capture efficiency. All lines fitted by eye.

zooplankton. However, it seems probable that grayling larger than 13 cm have difficulty retaining prey less than 1.5 mm in body length; this category encompasses all the strictly lake zooplankton such as *B. longirostris* and *D. l.* f. *typica*. It thus seems understandable that grayling larger than 13 cm appear to have little interest in zooplankton prey, and low reactive distance to small zooplankton.

MODE OF PLANKTIVOROUS FEEDING

At the low prey densities which occur in most arctic lakes grayling must usually feed on what they encounter rather than choosing particular sizes or species. The most common prey species in Toolik Lake rarely occur at densities greater than one or two per 10 L. However, as shown in Fig. 6, large grayling can find 2-mm prey in quite a large volume, particularly at high light intensities. Thus, one might expect to find very few large zooplankton in the top waters of these large arctic lakes but little difference in vertical distribution for the smaller forms. This is exactly what is found: lake *Daphnia middendorffiana*, often 2 mm in length, are almost never found above 5 m in Toolik Lake, which is about the midday 700- to 1000-lx depth, whereas the smaller *D. l.* f. *cephala* is commonly found even quite near the surface.

If arctic grayling are the major planktivorous fish in an arctic lake, the degree of planktivory will vary tremendously with fish size and light distribution. Perhaps this is why it was first shown in arctic systems that the level of planktivory rather than just the presence or absence of planktivorous fish was important to zooplankton communities (Nilssen and Pejler 1973). Regardless, given the extremely low densities of zooplankton in arctic lakes, it is clear that planktivory of this interesting and beautiful fish is of immense importance in the structuring and dynamics of zooplankton communities in these lakes.

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Structure–toxicity Relationship of Tin Compounds on Algae

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WONG, P. T. S., Y. K. CHAU, O. KRAMAR, AND G. A. BENGERT. 1982. Structure–toxicity relationship of tin compounds on algae. Can. J. Fish. Aquat. Sci. 39: 483–488.

The effects of a number of inorganic and organic tin compounds on pure cultures of green and blue-green algae and natural phytoplankton in lake water were tested. Organic tin compounds were generally more inhibitory to primary production and reproduction of the algae than inorganic tin compounds. The toxicity of organotin compounds varied considerably with the number and nature of the organic groups attached to tin, with trialkyl tin compounds being the most toxic forms. Within a given alkyl tin compound series, the longer the carbon chain, the higher the toxicity. A direct relationship between toxicity and partition coefficients of trialkyl tin compounds was observed. Other tin compounds had no such direct relationship.

Key words: algae, tin, toxicity, partition coefficients

WONG, P. T. S., Y. K. CHAU, O. KRAMAR, AND G. A. BENGERT. 1982. Structure–toxicity relationship of tin compounds on algae. Can. J. Fish. Aquat. Sci. 39: 483–488.

Nous avons évalué les effets de plusieurs composés stanneux inorganiques et organiques sur des cultures pures d'algues vertes et bleu-vert, et sur du phytoplancton naturel dans de l'eau de lac. Les composés stanneux organiques inhibent ordinairement la production primaire et la reproduction des algues à un degré plus élevé que les composés inorganiques. La toxicité des composés organiques varie beaucoup en fonction du nombre et de la nature des groupes organiques fixés à l'étain, les formes les plus toxiques étant les composés de la trialkyltine. Dans une série donnée de composés d'alkyltine, plus longue est la chaîne de carbone et plus grande est la toxicité. Nous observons une relation directe entre la toxicité et les coefficients de partition des composés de trialkyltine. Une relation directe de cette nature n'existe pas avec les autres composés stanneux.

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TIN and its compounds have been used since ancient times. In recent years they have been increasingly used in industrial, commercial, and agricultural areas. Inorganotin compounds play a role in the production of plating, printing, and food cans. Organotin compounds have wider applications. Diorganotin compounds are used as plastic stabilizers and lubricating oil additives; triorganotin compounds are used mainly as biocides in agriculture, paper, and paint industries. However, mono- and tetra-organotin compounds have minor industrial uses (Jensen 1977). In 1976, the annual world consumption of tin in all forms was around 180 million kg (Zuckerman et al. 1978). Most of these tin compounds are eventually released to the environment.

Once in the environment, the tin compounds are subject to photodegradation (Soderquist and Crosby 1978), chemical reactions (Zuckerman et al. 1978), and biological methylation (Huey et al. 1974; Ridley et al. 1977; Chau et al. 1980). Various tin compounds, including their degradation and methylation products, have been detected in significant levels in environmental samples around the world (Braman and Tompkins 1979; Hodge et al. 1979; Peterson et al. 1976; Chau et al. 1980).

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Toxicity of tin compounds to human beings (Fisher 1975) and terrestrial animals (Luijten 1972) has been extensively studied. In general, inorganotin compounds are not as toxic as the organic derivatives. The toxicity of organotin compounds varies considerably according to the number and nature of the organic groups, with tri- and tetra-alkyl tins being the most toxic forms. The increase in toxicity may be related to the insolubility of the chemicals in water. In fact, lipophilicity, as measured by the *n*-octanol/water partition coefficient, has been suggested as the most important parameter in bioaccumulation (Leo 1975) and toxicity (Schultz et al. 1980).

On the other hand, only limited data are available on the effect of tin compounds on aquatic biota, especially on algae (Jensen 1977). In this report, the effects of a number of inorganic and organic tin compounds on the primary production and reproduction of pure and natural algae were examined. The relationship between toxicity and partition coefficients was also studied.

Materials and Methods

ALGAL CULTURES

Three axenic algal cultures were used: *Scenedesmus quadricauda* (culture collection No. 11, Dr P. Healey, Fresh-

water Institute, Winnipeg, Man.), *Ankistrodesmus falcatus* var. *acicularis* and *Anabaena flos-aquae* (Ontario Ministry of Natural Resources, P.O. Box 213, Rexdale, Ont.). Each was grown in 100 mL of a modified CHU-10 medium (Chu 1942) at 20°C on a rotary shaker (100 rpm) under conditions of 18 h of light (5000 lx) and 6 h of darkness. No chelator (ethylenediaminetetraacetic acid) was added to the medium to avoid a high degree of chelation of the metals. Only the major nutrients, nitrate and phosphate, and some bicarbonate to buffer the medium to pH 8, were present. When the cells reached the logarithmic phase of growth (about 1 wk), they were used as inoculum.

Primary Productivity Experiments

Primary productivity was measured by the amount of ^{14}C-carbonate taken up by algae over a 4-h period. One millilitre of the culture ($\simeq 7 \times 10^5$ cells/mL) was added to 13.9 mL of CHU-10 medium containing various tin compounds at 0−50 mg as tin/L in a 25-mL Erlenmeyer flask. For those water-insoluble tin compounds (see under Chemicals section), equivalent volumes of acetone were used as controls. Acetone had no effect on primary productivity if the volume used was less than 0.05% of the medium. After a 24-h incubation at 20°C under conditions described above, a 0.1-mL aliquot of 7.4×10^4 Bq/mL ^{14}C-sodium carbonate (Amersham/Searle, 2.2×10^9 Bq/mmol) was added to each flask. The flasks were tightly capped with rubber stoppers wrapped in aluminum foil. A similar set of flasks was incubated in the dark. After further 4-h incubation, the cells were fixed with 0.05 mL of neutralized formalin. They were filtered through a 0.45-μm membrane filter and rinsed rapidly with 10-mL fresh CHU-10 medium to remove extracellular ^{14}C-sodium carbonate. Filters containing radioactive labeled cells were dissolved in 10 mL PCS scintillation counting fluor (Amersham/Searle). Radioactivity was measured by liquid scintillation counter with an automatic quenching factor and a 10 000 dpm upper limit. Radioactivity taken up by algae in the dark (<5% of total) was subtracted from the total radioactive counts. Radioactivity in the algae not exposed to tin compounds (control) was taken as 100%. The concentration causing a 50% reduction in primary productivity (median inhibition concentration, IC50) was estimated.

Toxicity of tin compounds on a natural algal community was tested with water from a sampling site in Lake Ontario near Hamilton, Ont. To compensate for the smaller number of algae, the volume of water was increased from 15 to 100 mL. One hundred and fifty microlitres of 3.7×10^5 Bq/mL ^{14}C-sodium carbonate was used. Other conditions were the same as in culture experiments.

Algal Reproduction Experiment

The effects of tin on reproduction (growth) of *A. falcatus* were measured spectrophotometrically with a Klett−Summerson Photoelectric colorimeter. One millilitre of the inoculum was added to 49 mL CHU-10 medium with and without tin compounds in a 300-mL Nephelo culture flask with side arm (Bellco Co., Vineland, NJ). At various intervals during incubation, the growth medium was tilted into the side arm which was then inserted into the colorimeter (with red filter No. 66). Because no medium is withdrawn from the flask for determination, this technique was more convenient and less prone to contamination. Klett units were converted to cell number using a standard curve relating klett units with cell number.

Chemicals

All tin compounds (from Alfa Division of Ventron Corporation, Danvers, MA) were in chloride form except triethyl tin bromide and bistributyl tin oxide (TBTO). For toxicity experiments, the compounds were dissolved in either glass-distilled water or acetone to make a stock solution of 10 000 mg Sn/L. Mono-, di- and tri-methyl tin and inorganic tin (IV) were prepared in water. All other compounds were in acetone.

Partition Coefficient Measurement

Partition coefficients of alkyl tin compounds between *n*-octanol and water were calculated from experimental data as the ratio of their concentrations in the two phases. The two solvents were presaturated with each other and allowed to equilibrate for about 2 d. The concentration used for the alkyl tin compounds was 500 mg/L of water or octanol. The solubility of the test compound in water and octanol determined the solvent to be used for making up the test solution. Appropriate volumes of the alkyl tin solution and the corresponding solvent were shaken in a 150-mL Teflon separatory funnel for 20−30 min, then centrifuged at 1200 rpm for 15 min, and the two phases separated.

The alkyl tin in each phase was determined by analysis of the total tin content by L'vov's platform−graphite furnace technique of atomic absorption, assuming that the test compound did not decompose in either solvent (L'vov 1978). The instrument parameters were: drying at 400°C for 40 s, charring at 800°C for 12 s, and atomizing at 2650°C for 15 s. Argon was used as sheath gas. The Sn-Electrodeless discharge lamp was operated at 9 W at the 224.6-nm line with deuterium background correction.

The partition coefficient (P) is defined as: $[\text{octanol}]_{Sn}/[\text{water}]_{Sn}$.

Results

Effects on *Scenedesmus quadricauda*

For *S. quadricauda*, inorganic tin compounds were relatively nontoxic (Fig. 1). Tin (II) had no effect on algal primary production even at levels as high as 50 mg/L. Tin (IV) was more toxic than tin (II). Its inhibitory effect was observed at 0.5 mg/L, and at 50 mg/L 50% inhibition of ^{14}C-uptake was noted. In contrast, organotin compounds showed much higher toxicity. Dimethyl and trimethyl tin compounds at 30 mg/L caused almost complete inhibition. A triphenyl tin compound was even more toxic. Its toxicity began at 0.05 mg/L, and at 0.5 mg/L, algal primary production was reduced to below 10% of the control. A tributyl tin compound was the most toxic tin compound tested; no uptake of ^{14}C-carbonate by algae was observed when the cells were exposed to 0.1 mg/L of it.

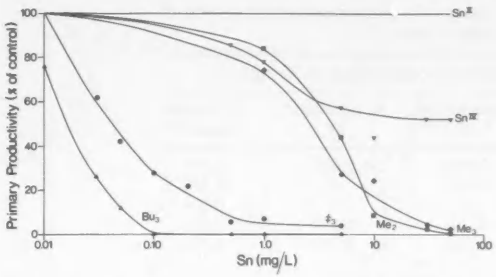

FIG. 1. Effects of tin compounds on the primary productivity of *S. quadricauda*. Sn^{II} and ^{IV} = inorganic tin chloride (II) and (IV); Me_2 and Me_3 = di- and tri-methyl tin chloride; Bu_3 = tributyl tin oxide; ϕ_3 = triphenyl tin chloride.

phenyl caused a drop in toxicity in the dialkyl tin compounds, but an increase in the trialkyl tin compounds.

Similar effects of tin compounds were observed when algal reproduction was used as the parameter. The results in Fig. 3 were from measurements taken after 8 d of incubation. They represented a typical response of the alga to tin. For trialkyl tin compounds, toxicity increased with an increase in carbon chain length. Furthermore, algal reproduction appeared to be more sensitive than primary production to tin toxicity. Triphenyl tin, at concentrations as low as 5 μg Sn/L, caused an 85% decrease in algal reproduction as compared with the control without tin exposure.

EFFECTS ON *ANABAENA FLOS-AQUAE*

The primary production of *A. flos-aquae* was also inhibited by the tin compounds. Trialkyl tin compounds were

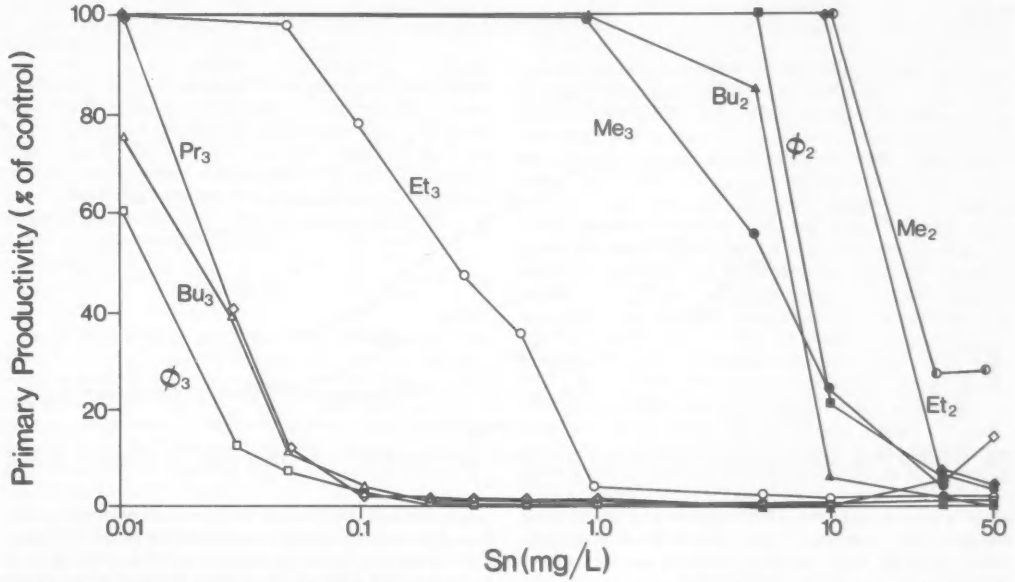

FIG. 2. Effects of tin compounds on the primary productivity of *A. falcatus*. Et_2 and Et_3 = diethyl tin chloride and triethyl tin bromide; Pr_3 = tripropyl tin chloride. Other symbols are in Fig. 1.

EFFECTS ON *ANKISTRODESMUS FALCATUS*

The toxicity of several tin compounds was tested with another common freshwater green alga. The results in Fig. 2 indicate that the toxicity again depended upon the forms and structure of the tin compounds. For primary production experiments, dialkyl tin compounds were not as toxic as trialkyl tin compounds. Triphenyl tin is not a trialkyl tin compound, but is included for comparison. Besides the effect of branch substitution, the carbon chain length also played an important role. In general, the longer the carbon chain length, the higher the toxicity. For example, the butyl tin compounds were more toxic than propyl, ethyl, and methyl tin compounds. Further increase in carbon chain length from butyl to

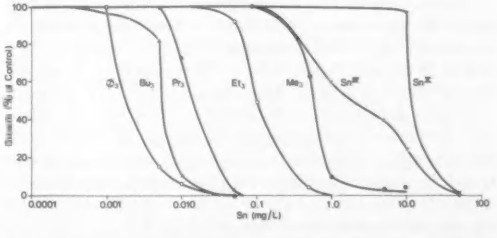

FIG. 3. Effect of tin compounds on the reproduction (growth) of *A. falcatus*. Data were from the 8th day of experiment. The symbols are explained in Fig. 1 and 2.

TABLE 1. Summary of IC50 of tin compounds on reproduction and primary productivity (PP) of pure algae and natural phytoplankton from Lake Ontario water.

Tin compounds	Reprod.	Medium inhibition concentration (IC50) mg/L			
		A. falcatus PP	*S. quadricauda* PP	*A. flos-aquae* PP	L. Ontario algae PP
Me_3Sn	0.570	5.500	2.600	> 5.000	0.350
Et_3Sn	0.100	0.200	0.100	—	0.055
Pr_3Sn	0.014	0.020	—	—	0.004
Bu_3Sn	0.005	0.020	0.016	0.013	0.003
ϕ_3Sn	0.002	0.010	0.040	0.020	0.002
Me_2Sn	—	21.000	4.100	> 5.000	—
Et_2Sn	—	16.000	—	—	—
Bu_2Sn	—	6.800	—	—	—
ϕ_2Sn	—	8.000	—	—	—
MeSn	—	23.000	—	—	—
BuSn	—	25.000	—	—	—
ϕSn	—	19.000	—	—	—
Sn (IV)	2.000	12.000	>50.000	>5.000	>50.000
Sn (II)	12.000	14.000	>50.000	>5.000	>50.000

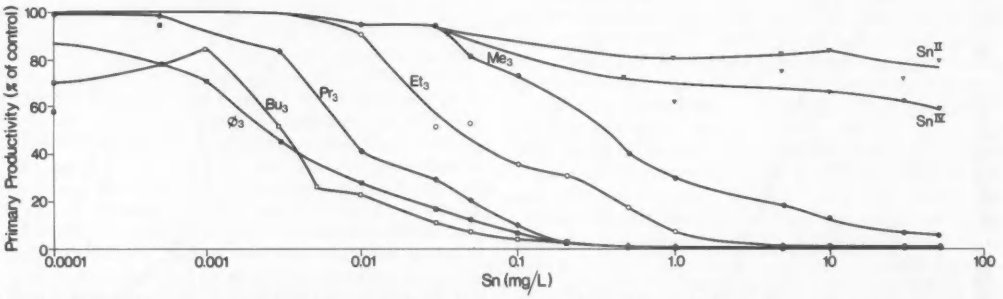

FIG. 4. Effects of tin compounds on the primary productivity of natural phytoplankton from Lake Ontario water. The symbols are given in Fig. 1 and 2.

again the most toxic forms. As the response was similar to the two previously mentioned algae, the results were not presented in graphic form, but were calculated and summarized in Table 1.

EFFECTS ON INDIGENOUS ALGAE IN LAKE WATER

The response of indigenous algae of water from a sampling station in Lake Ontario was tested to determine whether tin compounds had a similar inhibitory effect on primary production as in the pure algal cultures. The results (Fig. 4) show a similar pattern of toxicity. Inorganic tin (II) and (IV) were not very toxic as compared with trialkyl tin compounds. Increase in carbon chain length enhanced the toxicity on primary production, with triphenyl tin being the most toxic tin compound tested. In general, the indigenous algae seemed more sensitive to tin compounds than the pure algae. Triphenyl and tributyl tin compounds were toxic even at 0.1 μg/L.

IC50 OF TIN COMPOUNDS

Concentrations of tin compounds causing a 50% inhibition in reproduction and primary production of pure and indigenous algae were calculated and summarized in Table 1. These IC50 values were useful for quick comparison of toxicities. In *A. falcatus*, the values indicated that trialkyl tin compounds were the most toxic, followed by dialkyl, inorganic, and monoalkyl tin compounds. The reproduction and primary production of *A. falcatus* showed almost identical patterns, reproduction being slightly more sensitive to trialkyl tin toxicity. Primary production of indigenous algae from lake water was more sensitive to tin than pure cultures of green and bluegreen algae.

IC50 AND PARTITION COEFFICIENT RELATIONSHIP

The partition coefficients of various tin compounds in octanol−water were determined. Inorganic tin compounds (II and IV) and organic tin compounds with a 1 or 2 carbon chain length were relatively water-soluble whereas propyl, butyl, and phenyl tin compounds were soluble in octanol (Fig. 5). There was no indication that compounds more soluble in octanol would exert a higher toxicity to primary production of

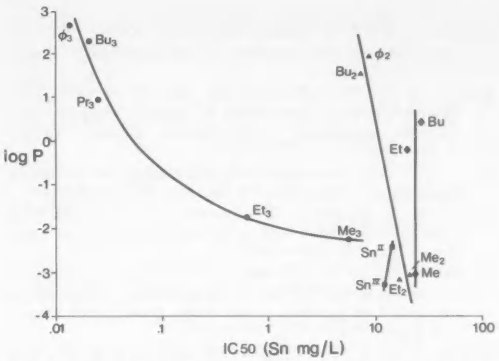

FIG. 5. The relationship between partition coefficients and IC_{50} of tin compounds on the primary productivity of *A. falcatus*. Me, Et, Bu = methyl, ethyl, and butyl tin chloride, respectively. Other symbols are explained in Fig. 1 and 2.

A. falcatus. On the other hand, it was quite clear that for the same degree of alkyl substitution, the longer carbon chain groups with higher solubility in octanol were more toxic to the algae (Fig. 5). The evidence was best exemplified in the trialkyl tin series where triphenyl and tributyl tin compounds were most soluble in octanol and had the highest toxicity as compared with triethyl and trimethyl tin compounds with low octanol solubility and low toxicity.

Discussion

The pure cultures of green and blue-green algae and the natural phytoplankton in lake water showed a remarkably similar response to tin toxicity (Figs. 1–4 and Table 1). The organic tin compounds were generally more toxic than inorganic tin compounds. The order of toxicity of the organic tin compounds in the freshwater alga, *A. falcatus*, was trialkyl > dialkyl > monoalkyl tin. Such an order of toxicity was also observed by Zuckerman et al. (1978) for terrestrial animals. Within a given alkyl tin compound series, the longer the carbon chain, the higher the toxicity, with phenyl and butyl being the most toxic forms for the alga (Table 1). As most of the trialkyl tin compounds are used extensively as biocides, almost all previous toxicity experiments were done with them. For trialkyl tin compounds, there are considerable variations in biological species responses to the length of the alkyl groups. For insects, trimethyl tins are most toxic; for mammals, the triethyl tins; for Gram-negative bacteria, the tripropyl tins; and for Gram-positive bacteria, fish, and fungi, tributyl tins show the highest toxicity (Smith 1978). The nature of the biological species differences to trialkyl tin toxicity is not known. Variations in bioassay techniques, such as in preparing the toxicants and in exposing the organisms, may account for some of the differences.

Most previous toxicity experiments on tin were performed with terrestrial animals, and not much is known about their effects on aquatic biota. Only a few papers have been published in this area and most of the work has been reported by Russian researchers. Jensen (1977) summarized the limited data on the toxic effects of organotin compounds to fish and showed that the LC50 level was in the range of 25–50 μg/L. At sublethal concentrations, triethyl tin chloride affected carbonate metabolism and other metabolic processes in the brain, liver, and muscle (Stroganov et al. 1974), as well as alkaline phosphatase, alanine aminotransferase, and cholesterol level in the serum of the common carp, *Cyprinus carpio* (Putintsev and Gameza 1980). For molluscs, trialkyl tin compounds as low as 3 μg/L were toxic (Polster and Halacka 1972) and 200–500 μg/L killed the organisms (Fisher 1975). Trimethyl and tribenzyl tin compounds were toxic to algae at 200 μg/L (Stroganov et al. 1966). This value is somewhat in between our values for pure cultures and natural lake water algae (Fig. 1–4).

Trialkyl tin compounds affect the oxidative activity of mitochondria (Fisher 1975), the central nervous system of sheep (Zuckerman et al. 1978), and the sulfydryl group of certain amino acids (Tan et al. 1978). The effectiveness of the trialkyl tin compounds may be related to the rapid absorption and accumulation of the compounds from water (Stroganov et al. 1974). The tendency of a chemical to be concentrated by an organism is dependent upon the partition behavior of the chemical between lipid and aqueous phases. The bioconcentration factors for chlorobenzenes and chlorophenols in trout muscles correlated well with the partition coefficient of these chemicals in the *n*-octanol/water system (Neely et al. 1974). For tin compounds, the solubility in *n*-octanol is a function of the number and molecular weight of organic groups attached to the tin atom: the higher alkyl tin compounds are soluble in *n*-octanol, but are relatively insoluble in water (Zuckerman et al. 1978). Our results show that compounds with a higher molecular weight than ethyl tin were more soluble in *n*-octanol whereas methyl and inorganic tins were more soluble in water (Fig. 5). Toxicity of some organophosphate pesticides decreased with increasing water solubility (Zitko 1975). However, we observed no such direct relationship between the solubility and toxicity of all tin compounds on *A. falcatus* (Fig. 5). Within trialkyl tin compounds, such direct relationships existed. Triphenyl, tributyl, and tripropyl tin compounds that were soluble in octanol were much more toxic than insoluble triethyl and trimethyl compounds. The relationship in di- and mono-alkyl tin compounds was less obvious.

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Spawning and Feeding Behavior of Captive Pacific Herring, *Clupea harengus pallasi*

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Laboratory observations indicate that spawning of Pacific herring (*Clupea harengus pallasi*) involves very similar if not identical behavior in males and females, and no identifiable behavioral interactions between the sexes. The presence of a sexual pheromone in herring milt is indicated because spawning behavior is rapidly initiated in ripe (ovulated and spermiated) herring of either sex following exposure either to herring milt or to a filtrate of ripe herring testes. Exposure to herring eggs or to filtrates of hake (*Merluccius productus*) or Pacific cod (*Gadus macrocephalus*) testes did not elicit such responses. Four components of spawning behavior induced by herring testis filtrate are identified and described: *rising and milling*, *papilla extension*, *substrate testing*, and *substrate spawning*. Testis filtrates also elicited *rising and milling* in spent, developing, and mature (unovulated and unspermiated) fish but *rising* was not followed by *papilla extension*, *substrate testing*, or *substrate spawning* in fish at these earlier stages of gonadal development. Herring at all stages of maturity also displayed *rising and milling* in response to an olfactory stimulus (filtrate of crushed euphausiids). This feeding response was weakest in the mature and ripe stages, when fish under natural conditions are reported not to feed, and was strongest in the spent stage, when wild fish resume feeding. In terms of the common components of the response to testis and euphausid filtrates (increased swimming speed, rising, and milling), differential responses to these two stimuli were seen only in ripe fish, suggesting herring at other stages of gonadal development may simply perceive milt as a food stimulus.

Key words: *Clupea harengus pallasi*, spawning behavior, pheromone, feeding

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Des observations en laboratoire indiquent que le comportement de ponte du hareng du Pacifique (*Clupea harengus pallasi*) est presque identique chez les mâles et les femelles, et qu'il est impossible d'identifier des interactions comportementales entre les sexes. Il existe un phéromone sexuel dans la laitance du hareng car il y a déclenchement rapide du comportement de ponte chez des harengs prêts à frayer (passé l'ovulation et la spermiation) de l'un et de l'autre sexe après exposition soit à de la laitance de hareng ou à un filtrat de testicules de harengs prêts à frayer. Par ailleurs, une exposition à des oeufs de hareng ou à des filtrats de testicules de merlu du Pacifique (*Merluccius productus*) ou de morue du Pacifique (*Gadus macrocephalus*) ne provoque pas de telles réponses. Nous identifions et décrivons quatre composants du comportement de ponte provoqué par un filtrat de testicules de hareng : *élévation et tournage en rond*, *extension de la papille*, *sondage du substrat* et *ponte sur le substrat*. Les filtrats de testicules provoquent également l'*élévation et le tournage en rond* chez des poissons vides, en voie de maturation et matures (avant ovulation et spermiation). Dans ces cas, cependant, l'élévation n'est pas suivie de l'extension de la papille, du sondage du substrat ou de la ponte sur le substrat chez les poissons à ces premiers stades de développement sexuel. Les harengs à tous les stades de maturité exhibent aussi le comportement d'élévation et de tournage en rond en réponse à un stimulus olfactif (filtrat d'euphausides broyés). Cette réaction nutritionnelle est la plus faible aux stades mature et prêt à frayer, quand les poissons dans des conditions naturelles ne se nourrissent pas. Elle est la plus forte après la ponte, quand les poissons sauvages recommencent à se nourrir. Si l'on mesure la

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réponse à des filtrats de testicules et d'euphausides en termes de composants communs (vitesse de nage accrue, élévation et tournage en rond), on ne l'observe que chez des poissons prêts à frayer, ce qui donne à penser qu'à d'autres stades de développement des gonades, le hareng peut simplement percevoir la laitance comme stimulus alimentaire.

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PACIFIC herring (*Clupea harengus pallasi*) spawn in the intertidal and subtidal zones along the British Columbia coast. Most of the spawn is deposited on vegetation at depths of less than 6 m (Haegele et al. 1979). The spawning season extends from February to June, with peak spawning activity in late March and early April (Hourston and Haegele 1980). Spawning fish are subjected to a short, intensive fishery to obtain ripe roe (ovulated eggs held within the ovaries) for the Japanese market (Hourston 1978). Forecasts of the abundance and timing of the runs to individual fishing areas play an important role in determining the location and extent of the fisheries to be permitted in any one season (e.g. Hourston 1979). Because the distribution of spawn among the various spawning grounds varies from year to year (Hourston et al. 1977), an understanding of spawning behavior could contribute to more effective fishery management. Such knowledge could also provide for better control of the timing of spawning in spawn-on-kelp operations, wherein impounded herring are induced to spawn on previously harvested kelp. Moreover, annual stock assessments are largely based on spawn deposition (Humphreys and Hourston 1978) and a knowledge of spawning behavior would be helpful in determining priorities for distribution of limited survey resources over potential spawning grounds.

Studies of spawning behavior of captive herring were undertaken during the 1975 and 1976 spawning seasons. Preliminary observations during the 1st yr of this study (Hourston et al. 1977) indicated that spawning behavior in female herring involves release of eggs when the fish is contacting a substrate with the paired fins and genital papilla. This behavior is repeated many times over a period of several hours and results in a pattern of egg deposition similar to that seen in natural conditions (Humphreys and Hourston 1978). Addition of herring milt rapidly induced spawning behavior in ripe female herring and also induced apparently identical behavior (involving milt release) in some males.

More extensive observations of milt-induced spawning behavior in ripe herring were conducted during the 1976 spawning season. The relationship between gonadal maturity and behavioral responsiveness to milt was examined by exposing spent, developing, and mature (but unripe) herring to milt at other times of the year. In addition, herring at each stage of gonadal maturity were exposed to an olfactory food stimulus (filtrate of crushed euphausiids) to differentiate between reproduction and feeding behaviors.

Methods

Herring were obtained from purse-seine sets in the southern part of the Strait of Georgia. Fish were transferred to small live tanks aboard the research vessel M/V *CALIGUS* for transport to the Pacific Biological Station. Ripe fish (ovulated and spermiated) caught between March and May suffered virtually no mortality. In contrast, the mortality in maturing fish obtained in January was very high (50–90%), despite considerable care in handling. This higher mortality was probably associated with the much higher incidence of scale loss in maturing than in ripe fish. Herring captured for the 1975 study (Hourston et al. 1977) and held for the subsequent year were also used.

Fish were held in circular fiberglass tanks of two sizes (245 and 180 cm diameter) provided with nonrecirculated seawater at ambient temperature (6–10°C) and salinity (27–31‰). Lighting was either natural daylight, or fluorescent light on a natural photoperiod. Although herring are reported not to feed during the spawning season (Taylor 1975), mature and ripe fish fed well in captivity. In 1975, the herring were fed frozen euphausiids for 1–2 wk after capture, and then weaned to 3-mm Oregon Moist Pellets (OMP). In 1976, fish were started directly on OMP after a week without food. Automatic feeders delivered OMP every 30 min for 8 h each day. Spent herring captured during the 1975 spawning season and fed only OMP matured and spawned in tanks during the 1976 season.

Prior to observation, fish were sexed and a number were tagged for identification. Ripe fish were sexed by applying gentle pressure to the belly to express eggs or milt from the gonopore. Unripe fish were sexed by macroscopic examination of a gonadal biopsy aspirated through the body wall (18-gauge hypodermic syringe) while the fish was anesthetized (MS222, tricaine methane sulphonate, 0.01%). A color-coded Peterson disc tag was then applied anterior to the dorsal fin and the fish returned to the holding tank. Ripe fish were not anesthetized before being tagged. No mortality or ill effects were observed in herring receiving these treatments.

Preparation and Use of Testis and Euphausiid Filtrates

Behavioral responsiveness to a filtrate of ripe herring testes was examined in fish at four stages of gonadal maturity: spent, developing, mature, and ripe (Table 1). To determine whether responses to testis filtrates differed from responses to a food stimulus, herring at each maturity stage also were exposed to a seawater filtrate of crushed euphausiids. Gonadal maturity stages as they relate to the International 'Hjort' Scale (Bowers and Holliday 1961) were assessed by macroscopic examination of dissected gonads. Spent fish (Hjort stage 7) have small gonads devoid of spermatozoa or vitellogenic oocytes. In developing fish (Hjort stage 3–4), the testes contain spermatozoa and the ovaries contain oocytes in which yolk is accumulating. Mature fish (Hjort stage 5) have large gonads equivalent in size to those of ripe fish (Hjort stage 6). The transition from the mature to the ripe stage in males is marked by an increase in fluidity of the milt (spermiation). In females, this transition is the result of ovulation, in which virtually all large vitellogenic oocytes first become translucent due to co-

TABLE 1. Stage of gonadal maturity, time of testing, time in captivity, and sex composition of small schools of herring (10 fish) exposed to ripe (spermiated) herring testis and euphausiid filtrates.

Maturity of test fish	Time of tests	Schools tested	Months in captivity	No. of tests with: Testis filtrates	No. of tests with: Euphausiid filtrates
Spent					
(Hjort stage 7)	June	All male	3	3	3
		All male	3	4	3
		All female	3	3	3
Developing					
(Hjort stage 3+4)	Oct.–Nov.	Male and female	8	6	7
		Male and female	8	3	4
		Male and female	8	2	4
Mature					
(Hjort stage 5)	Feb.–Mar.	Male and female	9	4	2
		Male and female	<1	6	4
		All male	<1	5	4
Ripe					
(Hjort stage 6)	Mar.–Apr.	All female	<2	2	2
		All female	<2	1	1
		All female	<2	2	3
		All male	<2	2	2
		All male	<2	4	4

alescence of yolk droplets, and then are released into the ovarian lumen as the follicles rupture.

Testis and euphausiid preparations were filtered to ensure that responses were induced by olfactory or gustatory rather than visual cues. Testis filtrates were prepared by forcing 40 g of herring testes (fresh or frozen) through a No. 600 nylon mesh and suspending the filtrate in 500 mL of cold seawater. Only testes from spermiated males were used to prepare filtrates. Frozen testes retained the ability to stimulate spawning for at least 1 yr. Euphausiid filtrates were prepared from commercially available frozen euphausiids. A 100-g frozen portion was thawed, crushed, and washed through the nylon mesh with 500 mL cold seawater. Testis and euphausiid filtrates were kept on ice until used for testing, usually within 2 h of preparation.

OBSERVATION OF BEHAVIOR

Spawning and feeding behavior were observed in a 16 000-L rectangular tank, 1.0 m deep, located in a small hut in an isolated area of the station grounds. The tank was supplied with nonrecirculating seawater (6–10°C; 150 L/min) and the inlet was positioned to create two opposing weak currents. Illumination was provided by four 80-W fluorescent lights positioned about 2 m above the water surface. Three full-height glass windows ran the length of one side of the tank; these were covered on the inside by removable plywood panels painted the same turquoise as the tank walls and bottom. A 1.2-m square mirror was mounted at 45° above the middle of the tank on the window side to permit simultaneous overhead and lateral observation.

Fish were observed from above the water surface through holes in a black screen running from ceiling to floor on the window side of the tank, and from below the water surface through small gaps between the adjustable plywood panels. Areas used for observation were kept in darkness, as even small visual disturbances, especially from below the water surface, usually altered schooling behavior.

Initial observations of spawning behavior in response to milt involved schools of varying size (from 10 to several hundred); however, as schools of 20 or more fish often formed several smaller schools, detailed observations of responses to testis and euphausiid filtrates employed only schools of 10 fish (males only, females only, or mixed sex; Table 1). As these small schools tended to swim around the observation tank near the walls at a fairly constant speed, series of elapsed times of uninterrupted circuits (16 m) were used to derive mean swimming speeds (m/s). In some cases where fish schooled but did not complete circuits of the tank, a second, less accurate method was used. The tank bottom was divided into six sectors and the mean number of sectors entered per minute by the lead fish was determined: multiplying this figure by 2.7 (complete circuit length/no. of sectors) provided a rough estimate of swimming speed.

Experimental fish were taken randomly from stock tanks and transported unanesthetized in plastic buckets to the observation tank. Tests were begun 1–2 d later when schooling behavior had become regular or, in the case of the mature fish tested in February–March, when the fish milled consistently in one area of the tank. Fish within a school swam at the same speed regardless of length and schools rarely were led by the largest individual. Consequently no attempt was made to standardize the size of test fish which ranged from ~ 16 to 20 cm standard length. Test schools were kept in the observation tank for not more than 5 d, during which time no food was given.

Tests were conducted between 10:00 and 16:00; there was no indication that either spontaneous activity or responsiveness to filtrates changed during this period. Prior to the addition of filtrates, fish were observed for at least 30 min to ensure that schooling behavior and swimming speed were stable and had not been affected by prior disturbance. When a base-line measure of prestimulation swimming speed had been obtained (usually at least 10 consecutive circuits of

the tank), addition of the filtrate by gravity feed at the inlet was begun as soon as the school passed the inlet. Thus, regardless of the direction of the school (clockwise or counterclockwise), filtrates had dispersed considerably before they were contacted. The five fastest consecutive circuit times attained by a school following detection of a filtrate were used to determine poststimulation swimming speed. Often, two filtrates (one testis and one euphausiid, or two of either) were tested during an observation period (about 3 h). In these cases, the second filtrate was not added until the school had returned to a stable swimming speed for at least 30 min. Usually, the period between addition of filtrates exceeded 60 min.

Results

Exposing ripe (ovulated or spermiated) herring to filtrates prepared from 40 g of ripe herring testes usually induced a standard sequence of responses which led to release of eggs or milt by at least some fish within a few minutes. A school swam slowly around the perimeter of the tank near the bottom and rose to or near the surface upon contacting the filtrate. This *rising* was usually accompanied by an increase in swimming speed, *milling* (a temporary cessation of schooling behavior), *extension* of the genital *papilla*, and the release of some milt. The fish then began to perform *substrate testing* behavior, contacting potential spawning substrates (tank walls and windows) with the tips of the paired fins. *Substrate spawning* behavior commenced when the fish contacted smooth, clear surfaces of suitable rigidity. The fish first oriented the ventral surface toward the substrate while swimming slowly and maintaining contact with the gular area and pectoral fins. The caudal region was then deflected dorsally, the papilla and pelvic regions brought in contact with the substrate, and a ribbon of milt or eggs extruded as the fish moved forward with rapid tail beats. Once *substrate spawning* behavior commenced, both sexes continued to release gametes between spawning acts. Milt tended to disperse in midwater, whereas eggs remained stuck together in a small clump behind the papilla until contact was again made with the substrate. Spawning acts occurred either singly, interspersed between periods of schooling behavior, or were performed in sequences of variable length.

The response to testis filtrates was the same for schools containing only males or females as for schools of mixed sex, confirming our previous findings (Hourston et al. 1977). In preliminary tests, spawning was induced by small amounts of milt (about 10 mL) expressed from spermiating males and added to the observation tank in the same manner as for testis filtrates. No attempt was made to determine the minimum amount of milt or testis filtrate required to induce spawning.

The addition of several other stimuli failed to induce spawning. These substances included seawater washes of dissected, ovulated herring ovaries, filtrates of maturing, unspermiated herring testes, and filtrates of hake (*Merluccius productus*) and Pacific cod (*Gadus macrocephalus*) testes of undetermined maturity.

Components of Spawning Behavior

Undisturbed schools of ripe fish (males, females, or both sexes tested together) swam in the lower half of the water column, usually within 10–20 cm of the bottom. Upon contacting the testis filtrate, the fish stopped schooling and formed a loose mill which moved to the surface within 10–30 s, i.e. *rising* and *milling* behavior. Usually the fish spread out after rising and, singly or in small temporary groups, swam rapidly in all areas of the tank, often breaking the surface with dorsal and caudal fins. Average swimming speed during this stage increased about 40% compared with prestimulation levels.

During the period of rapid surface milling, the genital papillae of both sexes, previously visible only as small bumps, began to protrude, reaching full extention within several minutes (Fig. 1 and 2). At this time, males often began releasing ribbons of milt up to 15 cm in length (Fig. 1) which began to disperse as they sank. In females, the papilla appeared to extend as rapidly as in the males; however, egg release was never observed until *substrate spawning* behavior commenced. Papilla extension was the most consistent aspect of the response to testis filtrates or milt and occurred in all 44 tests in which ripe fish were stimulated with filtrates prepared from males caught and frozen on the day they would have spawned. In the five tests in which papilla extension did not occur, testis filtrates had been prepared from spermiated males taken from the same population 7 d before spawning; the ineffectiveness of these preparations may have been due either to incomplete testicular maturation or to spoilage. When the reaction to testis filtrates did not lead to spawning, the papilla was slowly withdrawn and returned to the prestimulation size within ~ 20 min. During this time, the school reformed, moved from the surface to midwater, and its swimming speed decreased.

The onset of *substrate testing* behavior is subtle and was not recognized until spawning had been observed a number of times. Normally, schools of ripe fish swam close to the tank walls. Following the addition of testes filtrate, the fish moved closer to the wall until the tips of the pelvic and pectoral fins brushed against it. The fish apparently did not preselect spawning substrates and initially contacted all large surface areas as well as standpipes and several types of natural and artificial (plastic) vegetation. The fish showed no response following contact of the fins with either the tank walls or the plywood panels (both were painted but slightly rough). However, as the fins brushed against smoother surfaces such as the glass windows or metal standpipes, the fish turned on their side and oriented the ventral surface toward the substrate. Then, while keeping with the school, the fish contacted the substrate with the gular area and both pectoral fins, while the longitudinal axis was kept at approximately 15° from the substrate (Fig. 3a).

Although fish exposed to testis filtrate occasionally performed *substrate spawning* behavior during the first contact with the substrate, in most cases initial sequences of *substrate testing* were brief and did not lead to spawning. The fish simply moved off the substrate, resumed normal orientation, and continued swimming with the school. This interspersing of *substrate testing* with intervals of schooling occurred most often during initial stages of the response or when only a few fish in the school had reacted to the filtrate. When most of the fish in the school had been stimulated to perform *substrate testing*, the fish usually stopped schooling and performed series of such acts without leaving the vicinity of the selected

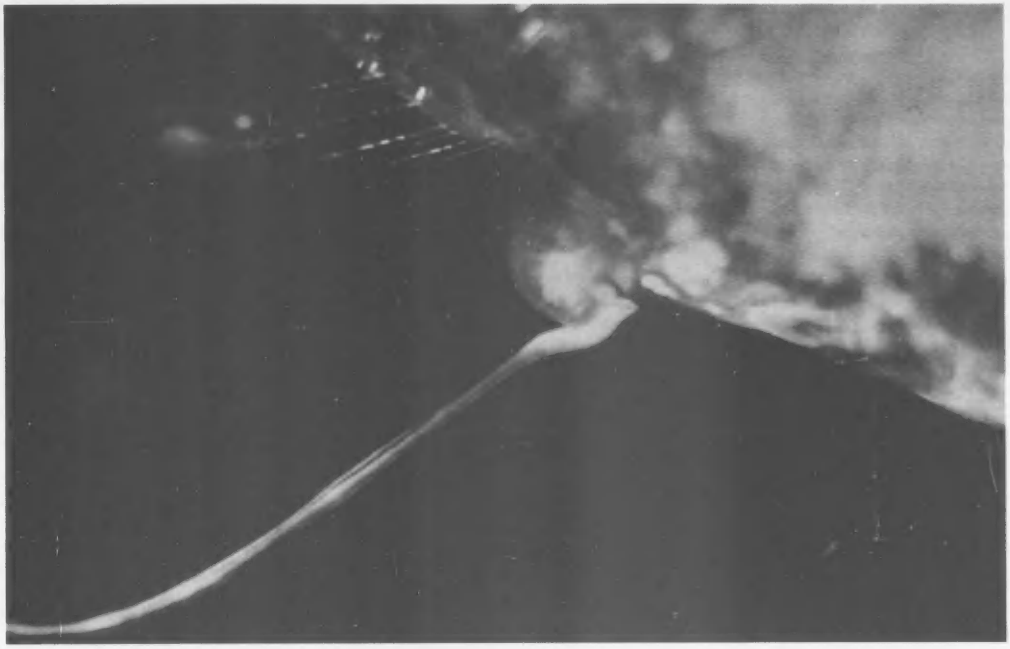

FIG. 1. Extended papilla of male herring showing release of milt ribbon.

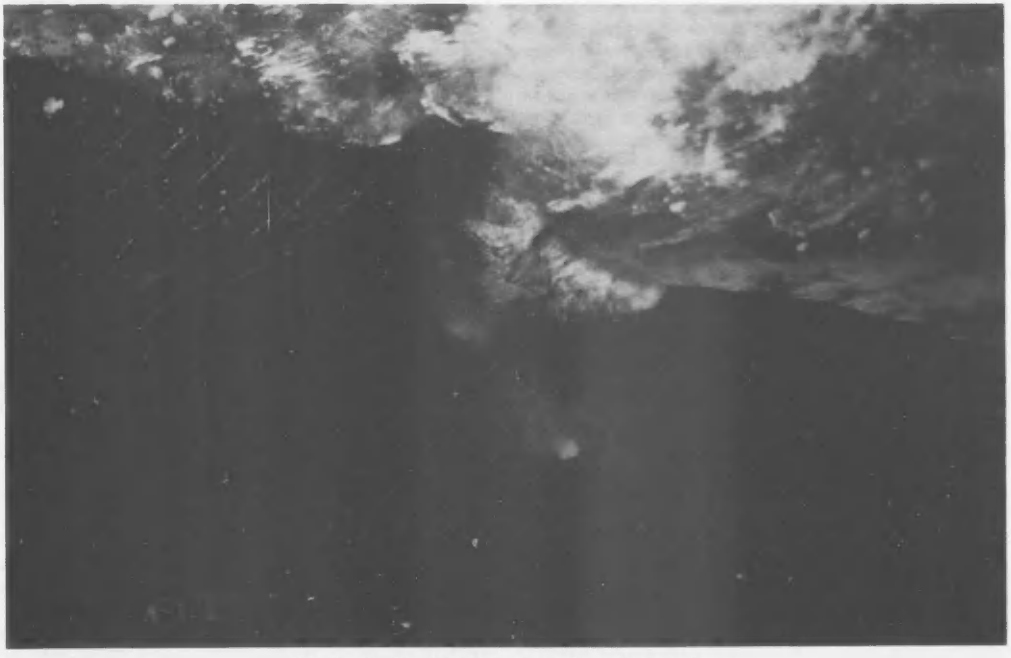

FIG. 2. Papilla of female herring with attached egg cluster.

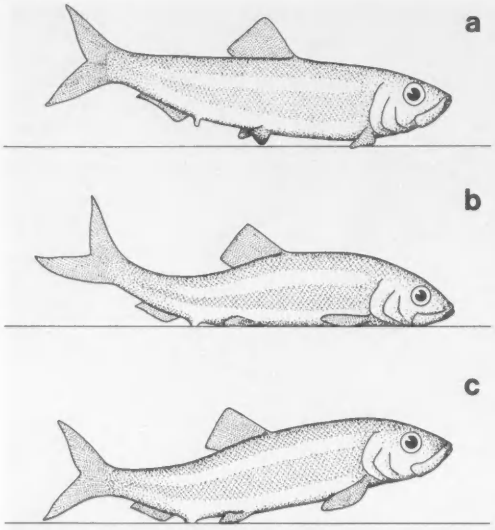

FIG. 3. (a) Herring with extended papilla performing *substrate testing behavior*. (b) *Substrate spawning behavior*. Note vertically deflected caudal region and contact of substrate by genital area and pelvic and pectoral fins. (c) Elevation of the anterior portion of the body at the end of an act of *substrate spawning behavior*.

substrate.

Both rigidity and texture appear to be important components of suitable spawning substrates. Fish were given a choice of 2-mil (1 mil = 25.4 μm) or 10-mil polyethylene plastic sheets mounted loosely on 1 × 1.3 m wooden frames placed against the tank walls. When there was no current and the sheets were slack, the fish performed *substrate testing* on both thicknesses but spawned only on the more rigid 10-mil plastic. When there was a current and the sheets were taut, spawning occurred on both thicknesses.

Fish never spawned on small beds (1 m^2) of *Zostera* or *Fucus* placed on the tank bottom, although both species are used as spawning substrates in natural conditions (Humphreys and Hourston 1978). In one test, some spawning occurred on a 1.5 × 2.0 m bed of artificial "*Zostera*" (clumps of 0.3-m strips of 6-mil green polyethylene). However, the majority of the spawning acts occurred on the standpipes and glass windows.

The transition from *substrate testing* to *substrate spawning* appears to be inhibited by sediment. On several occasions when the observation tank was heavily sedimented, ripe fish exposed to testis filtrates displayed normal initial responses (*rising* and *milling*, *papilla extension*, *substrate testing*) but failed to perform *substrate spawning*.

Substrate spawning is the altered body flexure and swimming activity shown by both male and female herring releasing gametes when in contact with a substrate. This term is used to differentiate this mode of gamete release from the release which occurs when the fish are not in contact with the substrate and display apparently normal swimming behavior. In the early stages of the response to herring testis filtrate, *substrate spawning* developed as an ongoing act of *substrate testing*. As spawning proceeded, fish tended to commence *substrate spawning* as soon as they contacted the substrate.

Substrate spawning began as a dorsal deflection of the caudal region and contact of the papilla and pelvic fins with the substrate (Fig. 3b). Simultaneously, the lateral amplitude of the tail movement decrease and the frequency increased. When the pectoral fins and gular area contacted the substrate intermittently, the anterior portion of the body was arched to a slight degree; when the pectoral fins and gular area were held against the substrate, arching of the body was more pronounced, producing a hunchback, hollow-belly effect. In the latter case, the mode of swimming was often modified further, the wave of contraction passing along the body not only decreasing in amplitude, but also increasing in frequency.

Usually, fish terminated an act of *substrate spawning* by raising the anterior portion of the body and swimming a short distance (10−20 cm) with the pelvic fins and papilla still contacting the substrate (Fig. 3c); as the papilla lifted from the substrate, the dorsally deflected caudal region returned to the normal position and the fish resumed normal swimming. However, acts of *substrate spawning* often ended with the fish returning to *substrate testing* (Fig. 3a). In this case, the anterior portion of the body remained in contact with the substrate while the posterior portion was elevated from the substrate and the caudal deflection lost. The duration of a *substrate spawning* act depended on the size of the substrate. On the longest continuous flat surface available (2.5 m), spawning acts frequently persisted for the entire length.

During *substrate spawning*, males usually released a ribbon of milt which, in the relatively still water of the observation tank, adhered to the substrate for as much as 3 d. Many males did not restrict milt release to periods of contact with the substrate but shed milt ribbons more or less continuously once *papilla extension* had occurred. Although egg release was not observed until females commenced *substrate spawning*, release usually continued in the intervals between such acts. In these cases, eggs released from the ovipore often adhered to the papilla or to previously released eggs, forming clusters of as many as several dozen eggs (Fig. 2). Egg clusters either were shed during normal swimming behavior or were attached to the substrate as the female began another *substrate spawning* act.

Females which spawned soon after capture deposited egg ribbons of various length and from one to four eggs in width. Some egg ribbons had a sine-wave pattern similar to that of milt ribbons, but most were relatively straight (Hourston et al. 1977). Nearly all our detailed observation of female spawning behavior involved females which had been ovulated at least a week. These fish deposited eggs either singly or in clusters but rarely in continuous ribbons as did recently ovulated fish. This difference in egg deposition pattern is thought to result from changes in the physical characteristics of ovulated eggs with time after ovulation, rather than from a modified form of *substrate spawning* behavior. This contention is supported by the observation that for most ovulated fish newly acquired from the field, slight pressure on the abdomen produced a "flow" of eggs from the ovipore, whereas for ovulated fish which had been held in the lab for several weeks, more pressure was required to release the eggs, which did not flow easily.

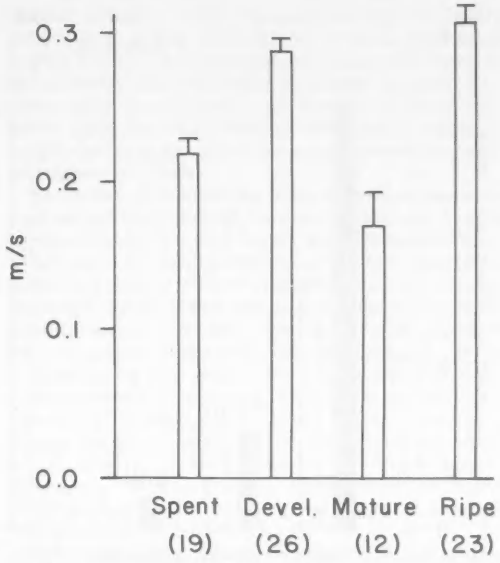

FIG. 4. Spontaneous activity (mean + SE) of small herring schools (10 fish; males, females, or mixed sex) at four stages of gonadal maturity. Sample size (parentheses) at each maturity stage obtained by pooling several determinations from several schools (see Table 1). With the exception of developing and ripe fish, all between-group differences are significant ($P < 0.05$; Kruskal-Wallace and Duncan's multiple range tests).

The spawning of small schools (10–20 fish) induced by herring testis filtrate was usually of short duration (less than 3 h) and ended before the fish had shed all their eggs or milt. In large schools (100–200 fish) of mixed sex, spawning was of longer duration (sometimes more than 12 h) and many fish released all gametes. It is likely that this effect of school size on the duration and completeness of spawning was due at least in part to the prolonged presence of stimulatory concentrations of suspended milt released by spawning males. In one unobserved spawning which occurred at night, only a few small egg clusters were attached to the tank walls. The majority of the eggs were scattered over the tank bottom as single eggs and small clusters, most not attached to the substrate. This suggests that egg release occurred when fish were not in contact with the substrate.

RESPONSES OF FISH AT DIFFERENT STAGES OF GONADAL MATURITY TO HERRING TESTIS AND EUPHAUSIID FILTRATES

The small schools of herring (10 fish) tested for responsiveness to herring testis and euphausiid filtrates are indicated in Table 1. In schools of spent, mature, and ripe fish, there was no indication that sex composition of the school influenced responsiveness; only schools of mixed sex were tested during the developing stage. Neither was there any indication that, at any stage of development, between-school differences in spontaneous activity or responsiveness to filtrates were greater than within-school differences on successive tests. For these reasons, the results from all schools at each maturity stage were pooled to determine average levels of spontaneous activity and responsiveness to filtrates.

Spontaneous activity (swimming speed) prior to addition of testis or euphausiid filtrates was lowest in mature herring tested in February and early March. In 13 of 25 pretest observations, mature herring did not school but formed a loose aggregation in which fish did not orient to others in the group. In the 12 pretest observations in which schooling occurred, the behavior was frequently interspersed with periods of nonschooling behavior. Consequently, the average swimming speed of 0.17 m/s (Fig. 4), which was based on the 12 tests in which schooling was observed, is a considerable overestimation of the spontaneous activity of the mature fish in our study.

The low incidence and sporadic nature of schooling in mature fish contrast markedly with the behavior of spent, developing, and ripe fish, which performed schooling in all 70 pretest observation periods. Schooling behavior was qualitatively similar for these three stages. Undisturbed schools swam around the observation tank near the walls and usually within 20 cm of the bottom. Schools often changed direction following a disturbance. Mean swimming speed of developing and ripe fish, the two most active groups, did not differ. All other between-group differences were significant (Fig. 4: $P < 0.05$; ANOVA, Duncan's multiple range test).

The addition of herring testis filtrate induced behavioral components specific to spawning (*papilla extension*, *substrate testing*, *substrate spawning*) only in ripe fish. The addition of euphausiid filtrate failed to induce these components of spawning in fish at any stage of maturity.

Behavioral changes occurring in response to both euphausiid and testis filtrates include increase in swimming speed and rising and milling. Based on these common responses, four degrees of response intensity are discernible: no response, swimming speed of the school does not increase and the school does not move toward the surface; stage 1 response, swimming speed of the school increases but the school does not move toward the surface; stage 2 response, swimming speed increases and the school rises in the water column but does not reach the surface; stage 3 response, swimming speed increases, the school moves to the surface, and schooling behavior may be disrupted. Euphausiid and testis filtrates both were capable of inducing the full range of response. However, the relative proportions of the four response intensities (Fig. 5) and the duration of the rising response (the time from the initial upward movement of the school until the school *began* its descent; Fig. 6) varied both with gonadal maturity and with the filtrate used. The degree of response to euphausiid filtrate was inversely related to gonadal maturity (Fig. 5) and this trend was was reflected in a significantly shorter duration of rising in mature and ripe fish than in spent fish (Fig. 6; Kruskall-Wallis, and multiple comparison test of Dunn 1964). In contrast with the effect of euphausiid filtrate, testis filtrate induced responses of equivalent intensity in ripe as well as in spent and developing fish (Fig. 5). Duration of rising in response to testis filtrate differed significantly not only between ripe and developing or mature fish, but also between spent and mature fish. Only ripe fish showed an obvious differential responsiveness to the two filtrates. In several tests of spent, developing, and ripe

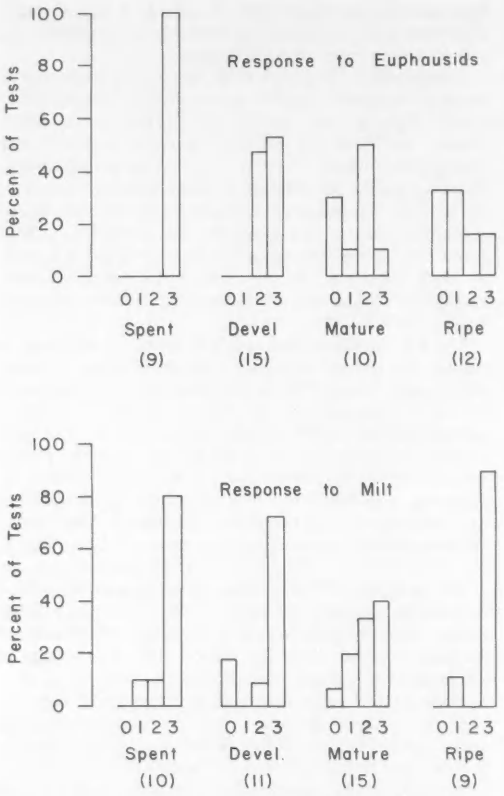

FIG. 5. Intensity of response to filtrates of euphausiids and spermiated herring testes in herring at four stages of gonadal maturity, based only on behaviors (increase in swimming speed, rising to the surface) which are common components of the response to milt and euphausiids. No response (0), the school neither increases swimming speed nor moves toward the surface; stage 1 response, swimming speed increases but the school does not move toward the surface; stage 2 response, swimming speed increases and the school rises in the water column but does not reach the surface; stage 3 response, swimming speed increases, the school moves to the surface, and schooling behavior may be disrupted.

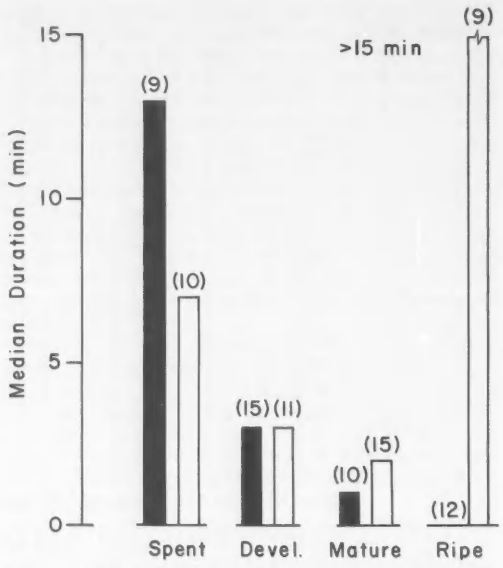

FIG. 6. Median duration of the rising response to filtrates of euphausiids (dark bars) and herring testes (light bars) in herring at four stages of gonadal maturity. Number of tests shown in parentheses.

schools, the addition of testis or euphausiid filtrates induced unmistakable feeding responses in some fish. These responses, which were not quantified, involved orienting to, and snapping at, floating bubbles and spots on the tank walls.

Discussion

SPAWNING BEHAVIOR

Our laboratory observations indicate male and female Pacific herring exhibit very similar if not identical reproductive behavior, spawning essentially as individuals independent of behavioral interactions with fish of the same or opposite sex. These findings are generally in agreement with the less detailed observations of Rounsefell (1930) and Schaefer (1937) on herring spawning naturally in Alaska and Puget Sound (Washington State), respectively. The major discrepancy among these studies concerns Rounsefell's description of apparent coordination between individual male and female herring, an activity which neither we nor Schaefer observed.

Natural spawnings differ from our laboratory situation in that the former involve the clouding of water with milt over a large area (Schaefer 1937; Hourston and Rosenthal 1976), and the blanketing of the substrate with eggs (Humphreys and Hourston 1978), rather than the deposition of discrete egg ribbons. These differences are considered to reflect mainly differences in the numbers of fish involved. During natural spawnings, wave action and currents would greatly accelerate the breakup and suspension of milt ribbons, creating a large, milky cloud in the water. Repeated spawning acts on the same portion of substrate would tend to obliterate egg ribbons deposited during initial acts. Nevertheless, it is also possible that under natural conditions the release of eggs in midwater rather than during contact with the substrate is more common than our laboratory observations suggest.

Two aspects of the natural spawning situation could result in more midwater egg release. The higher density of milt may induce a more intense behavioral response and a more rapid rate of egg release. Reduced visibility due to high concentrations of suspended milt would presumably increase the difficulty of locating a spawning substrate, and thus also increase the interval between successive acts of *substrate spawning*. As oviposited eggs rapidly lose their adhesive properties (personal observation; see also Alderdice et al. 1979), and mortality likely is lower in eggs attached to a

suitable substrate, herring spawning strategy presumably maximizes the proportion of eggs which are released during contact with the substrate. Indeed, our findings that herring in the laboratory apparently utilize tactile cues to identify substrates which are sufficiently rigid, smooth, and free of sediment suggest that similar behavior under natural conditions would account for the heavy utilization of marine vegetation as a spawning substrate.

Pacific and Atlantic herring (*Clupea harengus harengus*) share several basic similarities in spawning behavior. In both species spawning is a mass activity involving large numbers of fish and occurring over large areas of substrate. Both forms appear to be selective in the type of substrate used for egg deposition. Pacific herring and those Atlantic herring which spawn in shallow water deposit the majority of the spawn on marine vegetation (Tibbo et al. 1963; Hourston et al. 1977). Atlantic herring spawning in deeper water appear to select gravel substrates (Parrish et al. 1959; Caddy and Iles 1973; Drapeau 1973), although rock and clay bottoms are also used (Runnström 1941; Sameoto 1971). Mud bottoms apparently are not used as spawning substrates by Atlantic herring (Runnström 1941), and there is evidence from the present study that in Pacific herring sediment inhibits *substrate spawning* in response to herring milt.

Despite the similarities in spawning of Pacific and Atlantic herring, there appear to be significant differences between the behaviors of the two species. In Atlantic herring, only the female has been observed to perform the equivalent of *substrate spawning* behavior, releasing eggs while close to the substrate, but apparently neither contacting the substrate with the papilla nor exhibiting the body flexures seen in female Pacific herring (Ewart 1884; Holliday 1958). During egg release, female Atlantic herring alternate between moving slowly over the substrate and remaining stationary for as long as 2 min (Ewart 1884; Holliday 1958); this behavior has not been observed in Pacific herring. Spawning male Atlantic herring circle slowly above spawning females while releasing ribbons of milt but do not approach the substrate. Atlantic herring thus exhibit sex behavior dimorphisms which have not been observed in Pacific herring.

Responses to Testis and Euphausiid Filtrates

Ripe (spermiated and ovulated) herring held in a 16 000-L tank commenced spawning within minutes of the addition of herring milt or a filtrate of 40 g of ripe herring testes. In contrast, addition of ovulated herring eggs, euphausiid filtrate, or filtrates of testes from unspermiated herring or from hake (*M. productus*) or Pacific cod (*G. macrocephalus*) of undetermined maturity failed to induce spawning in ripe herring of either sex. It would, therefore, appear that the milt of Pacific herring contains a sexual pheromone (or pheromones) which stimulates behavioral and physiological responses leading to spawning in both sexes. By inducing milt release in ripe males which have not begun to spawn, the pheromone has the potential to amplify its stimulatory effect on spawning behavior.

Pheromones released by both male and female teleosts play a variety of functions in reproduction and reproductive behavior (Liley 1981). Although in some species male pheromones are present in urine and skin mucus (*Ictalurus* spp.; Rubec 1979) or are produced in specialized anal fin appendages (*Blennius pavo*; Lauman et al. 1974), there also is evidence for pheromones of testicular origin. For example, Losey (1969) suggested that male *Hypsoblennius* release a pheromone, perhaps during ejaculation, which facilitates courtship in other ripe males, and Okada et al. (1978) demonstrated that milt extracts rapidly induce male courtship behavior in the pond smelt, *Hypomesus olidus*. The situation in the herring, where milt stimulates equivalent sexual behaviors in both male and female, does not appear to have been described until now.

It is difficult to assess the role which milt might play in the spawning of herring under natural conditions. Milt may serve only to maintain or intensify spawning activity stimulated by factors yet to be identified. However, our laboratory observations demonstrate that natural spawning may be triggered by milt released from only a few fish. Such a release of milt, by inducing milt release in additional males, could activate a positive feedback mechanism capable of synchronizing the spawning behavior of large numbers of ovulated and spermiated herring in the presence of suitable substrate. This would account for the pattern of major spawnings in which spawning begins at one point on the shore and spreads out along the shore in one or both directions over the next few days. The initial release of milt may occur "spontaneously" in a few males in response to some specific environmental cue, or perhaps as the result of any one of a number of stressful factors (predation, commercial fishing operations) encountered on the spawning grounds (Hourston et al. 1977).

Only in ripe herring did exposure to herring testis filtrate induce physiological and behavioral responses normally restricted to spawning activities (*papilla extension*, *substrate testing*, *substrate spawning*). These responses were never induced by exposure to euphausiid filtrates. The addition of either testis or euphausiid filtrates induced a set of qualitatively similar responses (increased swimming speed, rising of the school toward the surface, disruption of schooling) in herring at all stages of gonadal development, but only in ripe fish did the intensity of these common responses to milt and euphausiids differ. This finding, and the observation that both testis and euphausiid filtrates occasionally induced feeding responses (orientation and capture attempts), suggests that spent, developing, and mature herring may simply perceive milt as a food stimulus. Restricting sexual responses to milt to the time of ovulation and spermiation obviously prevents inappropriate sexual responses in individuals incapable of reproducing successfully.

Our findings of seasonal differences in spontaneous activity and responsiveness to testis and euphausiid filtrates are consistent with current knowledge of herring behavior in the field. For example, in the spent stage (June) when herring in their natural habitat resume feeding near the spawning grounds before migrating to offshore summer feeding grounds, feeding responses of laboratory fish to euphausiid and testis filtrates are intense, and swimming speeds of undisturbed schools are moderate. In the developing stage (October–November), when herring normally migrate from offshore feeding grounds to inshore spawning grounds, our experimental fish exhibited increased spontaneous activity and somewhat decreased feeding responses to testis and euphausiid filtrates. Both spontaneous activity and re-

sponsiveness to filtrates were lowest in mature but unripe fish (February–March). It is significant that at this stage of gonadal development, when our captive fish performed schooling behavior only intermittently, herring in natural conditions are nonmigratory and are reported to "hold" for considerable periods in deep water close to the spawning grounds (Taylor 1964). In ripe fish (March–April), high levels of spontaneous activity and the resumption of schooling suggest the onset of behavior normally associated with rapid movement onto the spawning grounds. Responsiveness to euphausiids is lowest at this stage, a period when herring in natural conditions are reported not to feed.

Possible Management Implications

Our findings concerning the role of milt in inducing spawning behavior demonstrate that, in the presence of a suitable substrate, ripe fish may commence spawning within minutes of detecting herring milt. Papilla extension and rapid surface schooling are consistent components of the response to milt and may serve as practical indicators that spawning is imminent. The addition of milt suspensions to spawn-on-kelp pounds may provide a useful technique to induce spawning in ripe fish at the convenience of the pound operator. The demonstrated importance of the presence of suitable substrates in initiating spawning activity and the inhibiting effect of sedimented substrates provide a useful basis for the identification of potential spawning grounds.

Acknowledgments

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NOTES

Predation of Sea Scallops (*Placopecten magellanicus*) by Lobsters (*Homarus americanus*) and Rock Crabs (*Cancer irroratus*) in Underwater Cage Enclosures

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JAMIESON, G. S., H. STONE, AND M. ETTER. 1982. Predation of sea scallops (*Placopecten magellanicus*) by lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) in underwater cage enclosures. Can. J. Fish. Aquat. Sci. 39: 499–505.

Predation studies in underwater cage enclosures on natural substrates were conducted in 1979 and 1980 to assess the propensity of adult American lobsters, *Homarus americanus*, and rock crabs, *Cancer irroratus*, to prey upon sea scallops, *Placopecten magellanicus*. In 1979, the initial prey by both predator species was large, embedded horse mussels (*Modiolus modiolus*). In the enclosure containing lobsters, this was followed by lobster cannibalism and, finally, when lobster density was reduced, predation on large sea scallops (80–110 mm shell height). No cannibalism or predation on large scallops occurred in the rock crab enclosure. In 1980, small scallops (40–55 mm shell height) were presented to lobsters and rock crabs; predation occurred regardless of predator density. Large sea scallops and unembedded horse mussels were consumed when crustacean densities approached natural levels. These studies demonstrate that small sea scallops and embedded horse mussels can be readily consumed by lobsters and rock crabs under field conditions, but that natural predation of large scallops by either rock crabs or lobsters is of lesser magnitude.

Key words: sea scallops, crabs, lobsters, predation, prey selectivity

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La prédation du homard, *Homarus americanus*, et du crabe commun, *Cancer irroratus*, sur le pétoncle géant, *Placopecten magellanicus*, a été étudié en 1979 et 1980 à l'aide de cages sous-marines placées sur des substrats naturels. En 1979, les proies initiales des deux espèces prédatrices sont de gros modioles du nord (*Modiolus modiolus*) enfouis. Dans l'enceinte des homards, ceci est suivi de cannibalisme et, finalement, une fois la densité des homards réduite, de prédation sur de gros pétoncles géants (80–110 mm de hauteur de coquille). Dans l'enceinte des crabes communs, il n'y a ni cannibalisme ni prédation sur de gros pétoncles. En 1980, nous avons offert aux homards et aux crabes des petits pétoncles (40–55 mm de hauteur de coquille); il y a alors prédation, indépendamment de la densité des prédateurs. C'est au moment où la densité des crustacés se rapproche des niveaux naturels que les gros pétoncles et les modioles non enfouis sont consommés. Ces études démontrent que des pétoncles géants de petite taille et des modioles enfouis peuvent facilement être consommés par le homard et le crabe commun dans des conditions naturelles, mais que la prédation naturelle sur les gros pétoncles est de moindre ampleur.

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PREVIOUS reports on predation of sea scallops (*Placopecten magellanicus*) under natural conditions have been largely anecdotal or based on stomach analyses (Squires 1970), with no field experiments. Caddy (1968, 1973) reported a number of invertebrate and vertebrate species as probable predators of scallops damaged during trawling and dredging, and Dickie and Medcof (1963) cited starfish (*Asterias vulgaris*) and moonsnails (*Lunatia heros*) as natural predators able to capitalize on scallops made vulnerable by temperature debility. Medcof and Bourne (1964) identified starfish (*A. vulgaris*, *Crossaster papposus*) and a number of fish species as natural predators of scallops. Predation of scallops by rock crabs (*Cancer irroratus*) and American lobsters (*Homarus americanus*) under laboratory conditions was reported by Elner and

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TABLE 1. The mean size (mm ± SD) and number of each of the experimental species added to the corrals.

1979 Study

Lobster corral			Crab corral		
Species	*n*	Size	Species	*n*	Size
Scallop (Aug. 3, 4)	26	101.4±11.7	Scallop (Aug. 3, 4)	24	103.1±9.3
Lobster	59	77.2±12.2	Crab	49	111.7±8.1
Scallop (Aug. 21)	22	—[a]	Scallop (Aug. 21)	30	—[a]

[a]Combined size (n = 52): 77.7 ± 28.1.

1980 Study

Corral 1			Corral 2		
Species	*n*	Size	Species	*n*	Size
Scallop (<70 mm height)	81	46.9±5.6	Scallop (<70 mm height)	64	49.4±7.9
Scallop (≥70 mm height)	21	90.7±11.3	Scallop (≥70 mm height)	22	92.5±8.8
Lobster	19	94.5±11.9	Rock crab	8	111.1±11.7
Horse mussel	22	80.8±8.4			
Rock and green crabs	31	63.8±20.9			

Corral 3			Corral 4		
Species	*n*	Size	Species	*n*	Size
Scallop (<70 mm height)	107	47.7±6.4	Scallop (<70 mm height)	114	48.1±7.0
Scallop (≥70 mm height)	30	91.1±8.7	Scallop (≥70 mm height)	41	94.4±10.2
Lobster	14	93.9±11.3	Lobster	53	91.7±9.2

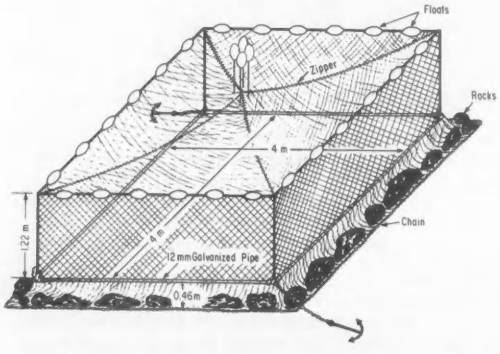

FIG. 1. The underwater cage design employed in this study.

Jamieson (1979).

In the Northumberland Strait, sea scallops are widely distributed (Caddy et al. 1977) and support a commercial fishery (Jamieson et al. 1981). The distribution of both rock crabs and lobsters commonly overlaps that of scallops (Stasko et al. 1977). These species also occur along the Atlantic coast of Nova Scotia, although their distributions are perhaps more contagious because of greater variability in substrate type, exposure, and depth.

Given that rock crabs and lobsters are potentially significant predators of scallops in nature and may affect the availability of scallops to the commercial scallop fishery, field experiments utilizing relatively large underwater enclosures were conducted to determine under what conditions predation of scallops might occur.

Materials and methods — In 1979, experiments were conducted in Northumberland Strait with large scallops (80−110 mm shell height) as prey (Table 1). In 1980, experiments were conducted in St. Margaret's Bay, Nova Scotia, using as prey both small (40−55 mm shell height) and large scallops (Table 1).

Underwater corrals (Fig. 1) 4 × 4 × 1.2 m were constructed from 1.5-inch (38-mm) stretch nylon mesh attached to a frame of galvanized piping. A mesh skirt 46 cm deep with galvanized chain at its outer perimeter extended outwards from each corral; the top of the corral was covered with zippered, 2-inch (57-mm) stretch, knotless nylon mesh.

TABLE 2. Additions, mortality due to predation, and abundance of each experimental species in each corral during the 1979 study period. OS = observed count; M = mortality; A = additions; T = total. Starting date: July 31, 1979.

Day No.	Lobster corral							Rock crab corral					
	Scallop				Lobster			Scallop			Rock crab		
	OS	M	A	T	OS	A	T	OS	A	T	OS	A	T
2						4	4						
3			7	7					12	12			
4	7		19	26	3	6	9	12	12	24		24	24
7	26			26	6	15	21	24		24	18		18
9	26			26	13	9	22	24		24	10	4	14
16	26			26	10		10	24		24	10		10
17	26			26	10	6	16	24		24	8	10	18
22	26		22	48	9	12	21	24	30	54	10	23	33
28	48			48	9[a]	12	21	54		54	16	19	35
43	47	1		47	3		3	54		54	7		7
50	38	9	—	38	1	—	1	54*	—	54	4	—	4
Total		10	48			64			54			80	

[a]Evidence of lobster cannibalism.

When deployed, crustacean escape was restricted by closing the cover and piling rocks on the skirt. The three-dimensional integrity of the structure was maintained by buoys attached to the tops of the walls and the center of the cover.

1979 studies — Three corrals were deployed August 1, 1979, 3.5 km offshore in eastern Northumberland Strait (45°40′40″ N, 68°04′50″ W) in 13.7 m of water. The scallops, lobsters, and rock crabs placed in the corrals were caught within 3 km of the study location and were added to the corrals within 1 h of capture. Measurements (Table 1) were made of carapace length (back of eye socket to posterior margin) for lobsters, maximum carapace width (excluding perimeter spines) for rock crabs, and height (edge of hinge to distal edge of the valves) for scallops. One corral contained only scallops as a control study; no scallop mortality occurred. Because scallop predation by rock crabs and lobsters was known to be size specific (Elner and Jamieson 1979), additional large scallops which averaged smaller than those initially introduced were added to both corrals containing crustaceans on August 21 in an effort to facilitate predation (Table 2). The numbers, and in some instances sizes, of each species present in the corrals were recorded by divers at least once weekly and any signs of scallop damage or mortality noted. No "wild" lobsters or crabs from outside the corrals were observed to enter a corral. After 2 wk of observation, many horse mussels (*Modiolus modiolus*) had been eaten; divers then removed the remaining horse mussels (58.7 and 40.4 kg wet weight from the crab and lobster corrals, respectively) in an effort to initiate scallop predation. Only the three experimental species, lobster, crab, and scallop, were left in abundance.

Because the corrals were open on the bottom, the natural substrate and existing benthic fauna were accessible to the introduced species. The bottom substrate was gravel with occasional small boulders, covered with a thin layer of fine sediment. Prior to commencement of the study, four random 0.5-m^2 quadrat samples were collected from around the corrals and the fauna identified and measured (Table 3). Scallop and crustacean densities in the immediate area of the corrals were low, with approximately one scallop per 50 m^2 and rock crabs and lobsters only occasionally being sighted during daylight dives. To provide cover for the lobsters, 6-inch (0.15-cm) diameter, clay drainage tiles were placed in the lobster corral. Maximum tidal current velocities were less than 0.1 m/s (the minimum sensitivity of our flowmeter) and diver visibility averaged 2–3 m. Continuous bottom temperature readings were recorded with an underwater temperature recorder (Ryan model "J"). During the course of the study, temperatures ranged from 13.3 to 17°C, with an average of 14.9°C (graphically illustrated by Dobson et al. (1981a)). The experiment terminated September 18, 1979.

TABLE 3. Benthic fauna collected in four 0.5-m^2 quadrat samples from around the two corrals in 1979.

Quadrat	Species	*n*	Size (mm ± 1 SD)
1	*Modiolus modiolus*	7	74.9±29.5[a]
2	*Modiolus modiolus*	39	83.9±11.5[a]
	Strongylocentrotus droebachiensis	4	24.3±17.4[b]
	Asterias sp.	1	23[c]
3	*Modiolus modiolus*	24	81.0±17.3[a]
	Strongylocentrotus droebachiensis	20	44.5±9.8[b]
	Ophiopholis sp.	10	
	Balanus sp.	6	
4	*Modiolus modiolus*	10	87.6±8.1[a]
	Strongylocentrotus droebachiensis	4	35.5±11.5[b]
	Buccinum sp.	2	53.0±11.0[a]

[a]Length.
[b]Diameter of test.
[c]Radius.

1980 studies — Four corrals identical with those used in 1979 were deployed on July 25, 1980, 0.3 km off Boutilier's Point in St. Margaret's Bay, N.S. (46°39′02″ N, 63°57′02″ W) in 10 m of water. Except for the sea scallops which were collected on Georges Bank, all experimental species were col-

TABLE 4. Abundance (T), predator additions (A), and number of prey eaten (M) for the main experimental species in each corral during 1980. T^1 = abundance after predator addition; T^2 = prey abundance before predation.

Lobster corral No. 1

Day No.	Lobster A	Lobster T^1	Scallop Small M	Scallop Small T^2	Scallop Large M	Scallop Large T^2	Horse mussel M	Horse mussel T^2
1	4	4						
4		2		40				
8	2		1	40				
11			2	39				
13		1						
24		1	18	38				
26								20
27		1	19	37				
30	3	4						
34	2							
38		3						
40	1	4						
41			18	38				
44	3	1	1	19		10		
48			9	18	1	10	2	20
55	4	4	9	15	3	9		
62		2			1	17		
69		0		6		16	6	20

Crab corral No. 2

Day No.	Rock crab A	Rock crab T^1	Scallop Small M	Scallop Small T^2	Scallop Large M	Scallop Large T^2
1	4	4				
4		4		40		
8		4	2	40		
26		4	15	39		
31	4					
39			7	40		
43		6	9	33		
45						9
51		5	11	24	2	9
54			1	21		
58		2	5	22		
61		2	3	27	1	7
74		2		24	1	17

Lobster corral No. 3

Day No.	Lobster A	Lobster T^1	Scallop Small M	Scallop Small T^2	Scallop Large M	Scallop Large T^2
1	2	2		40		
4	2	2				
11		2	17	40		
17		0	27	40		
21	2	2				
25		1	2	25		
29		1	26	39		
31		1	2	13		
32	1	2				10
35		0	4	27		
37	2	2				
39			2	37		
43		0	4	37		
46	2	2	5	33		
53		0	8	32	2	10
60	2	2	4	26	2	8
74		1		22		6

Lobster corral No. 4

Day No.	Lobster A	Lobster T^1	Scallop Small M	Scallop Small T^2	Scallop Large M	Scallop Large T^2
1				40		
7	15	15				
9		5	28	49		
17	10	14	25	25		
19				30		10
22	4	6	22	30	1	10
24	10	14	5	8		
26			18	25	2	10
30		5	7	7	5	8
33	9	9			2	9
40	5	5	6	9	3	28
53		2		3		25
61		1		3		25

lected within 3 km of the study site. Twenty control scallops held adjacent to the corrals in a cage which protected them from predation showed no mortality. Drainage tiles were again provided to give cover for the lobsters. An effort was made to maintain both prey and predator densities at initially established levels, with observations at least once weekly. No molluscs escaped the corrals, but crustacean escape was common.

In corral 1, the initial objective was to determine if small scallops could be successfully preyed upon by lobsters at a high lobster density (initially 0.25 lobsters/m^2). Small scallop predation was shown to occur readily, and so after 26 d, large scallops and three other potential prey species, horse mussels, juvenile rock crabs, and green crabs (*Carcinus maenas*), were added to the corral to determine the relative preference of scallops as prey in the presence of other potential prey species.

In corral 2, the objective was to quantify predation of both small and large scallops by mature rock crabs at a high density (initially 0.38 crabs/m^2). Initially, only small scallops were provided, but after predation was shown to occur readily, large scallops were also added to this corral.

In corrals 3 and 4, the objectives and procedures were similar to those used with corral 2, except that lobsters were the predators, and predator density was moderate (initially 0.13 lobsters/m^2) and very high (initially 0.94 lobsters/m^2), respectively.

As in the 1979 study, the corrals were open on the bottom, making available to the experimental species the natural substrate and benthic fauna. The bottom substrate was sand with occasional medium (5- to 15-cm-diameter) to large (>15-cm-diameter) rocks, all covered with a thin layer of particulate matter. Sampling of the benthic fauna in corral 1 indicated that the only indigenous potential prey species were small sea urchins (*Strongylocentrotus droebachiensis*). In a complete sampling of all macrobenthos in corral 1 prior to introduction of the experimental species, 78 sea urchins, averaging 3.3 mm (SD = 0.8 mm) in test diameter, were observed (average density = 4.9/m^2). Because of their small size, diver-caused water turbidity during observation, and the tendency of sea urchins to be confined to rocks, actual sea urchin density in the corral may be underestimated. Tidal currents were minimal, diver visibility averaged 5–6 m, and benthic water temperatures, graphically illustrated by Dobson et al. (1981b), ranged from 5.6 to 17.4°C, averaging 11.6°C, during the study period.

Results — 1979 study — The corrals used retained the decapods studied for an acceptable time frame, with the nine lobsters for which we have observations being retained for an average of 12.4 d (SD = 6.3 d).

The densities of scallops, rock crabs, and lobsters inside the corrals were established much higher than was found in the immediate area outside the corrals in an effort to increase predation rate. Initial predation by both crustacean species appeared confined to horse mussels, which occurred at an average density of about 40/m^2 immediately outside the corral. No scallops showed any sign of crustacean attack, i.e. cracked or chipped valves, while horse mussels were present. No evidence of sea urchin predation was observed.

An effort was made to maintain predator numbers continuously in each corral at about 24 animals; but regardless of number of each predator species added, the number remaining at the next observation period was usually considerably reduced (Table 2). Initially, this reduction appeared to result only from rock crab and lobster escape but after the removal of the mussels, cannibalism began to occur in the lobster corral. Lobster remains were observed at the entrances to the drainage tiles, and although they could perhaps have resulted from lobster moulting no recently moulted lobsters were observed in the corral. No crab cannibalism was evident.

The first evidence of scallop predation occurred on September 11, 25 d after the mussels had been removed, when one chipped scallop shell was found in the lobster corral. Lobster density had been allowed to decline prior to terminating the experiment, and only three lobsters were present. By September 18, only one lobster remained, but an additional nine scallops had been eaten (Fig. 2).

1980 study — On the basis of the 1979 study, two changes in experimental design were incorporated into the 1980 study. First, small scallops were also provided as prey to facilitate potential predation, and, second, two lobster corrals were maintained with a more moderate density of lobsters in an effort to minimize possible interference between predators during the predation process.

Predation of small scallops was high, with 94, 93, and 100% of the introduced scallops being eaten in corrals with initial lobster abundances of 2, 4, and 15 lobsters, respectively. Sixty-eight percent of the introduced small scallops were eaten in the rock crab corral. In contrast, predation of large scallops was significantly less, with only 13, 25, and 32% of these scallops being eaten in corrals with initial lobster abundances of 2, 4, and 15 lobsters, respectively, and 20% of these scallops being eaten in the rock crab corral.

In corral 1, where four potential prey species were present during part of the study, only the scallops and horse mussels were eaten. No evidence of crab remains was found (11 rock crabs and 20 green crabs were added between days 26 and 38), and it is felt that the crabs likely escaped from the corral, particularly in the case of the green crabs. Thirty-six percent of the horse mussels provided were eaten. However, in contrast with the 1979 study in which horse mussel predation was extensive, the horse mussels available for predation in 1980 were not embedded in the substrate, but lay loosely on it.

No evidence of sea urchin predation was observed, but with the small size of sea urchins present, it would likely be minimal. There was no evidence of lobster or crab cannibalism.

Discussion — The results of these experiments may be specific to the unique conditions described. Nevertheless, as a first attempt to perform field predation studies with rock crabs, lobsters, and scallops on a natural substrate, the results provide insight into decapod predation and how various sizes of scallops may rank as prey items. Also, although unintentional and impeded, decapod escape occurred, which allowed each predator species to influence its own density. Escape was never observed but is presumed to have occurred under the mesh skirt. Previous studies by Breen (1974) utilized relatively small, closed cages (2 × 1 × 1 m) with a plywood floor which precluded direct contact of lobsters with the natural substrate. As a result, opportunity for the lobsters, which had been previously starved for 2–6 wk, to select alternative prey items other than the two species presented was eliminated. The basic design of our study was to maintain lobsters and rock crabs in contact with scallops to investigate under what conditions natural scallop predation might occur. Thus, by allowing the presence of other potential benthic prey species it became evident that although large scallops could be eaten, their initial preference as a food item by both rock crabs and lobsters is probably low. Large horse mussels (60–90 mm height), which Breen (1974) suggested could not be physically opened by lobsters, were the initial prey by both rock crabs and lobsters in the 1979 study. Following the removal of the mussels, cannibalism occurred among the lobsters before large scallops were consumed.

In 1980, predation of small scallops was intensive at all lobster densities, but as in 1979, predation of large scallops was generally correlated with low lobster abundances. Because of frequent escapement, lobster densities at the time of predation on large scallops are unknown. When both scallop size-classes were present simultaneously, small scallops showed the greatest mortality.

A low rate of predation on large scallops was expected, as Elner and Jamieson (1979) demonstrated that relative

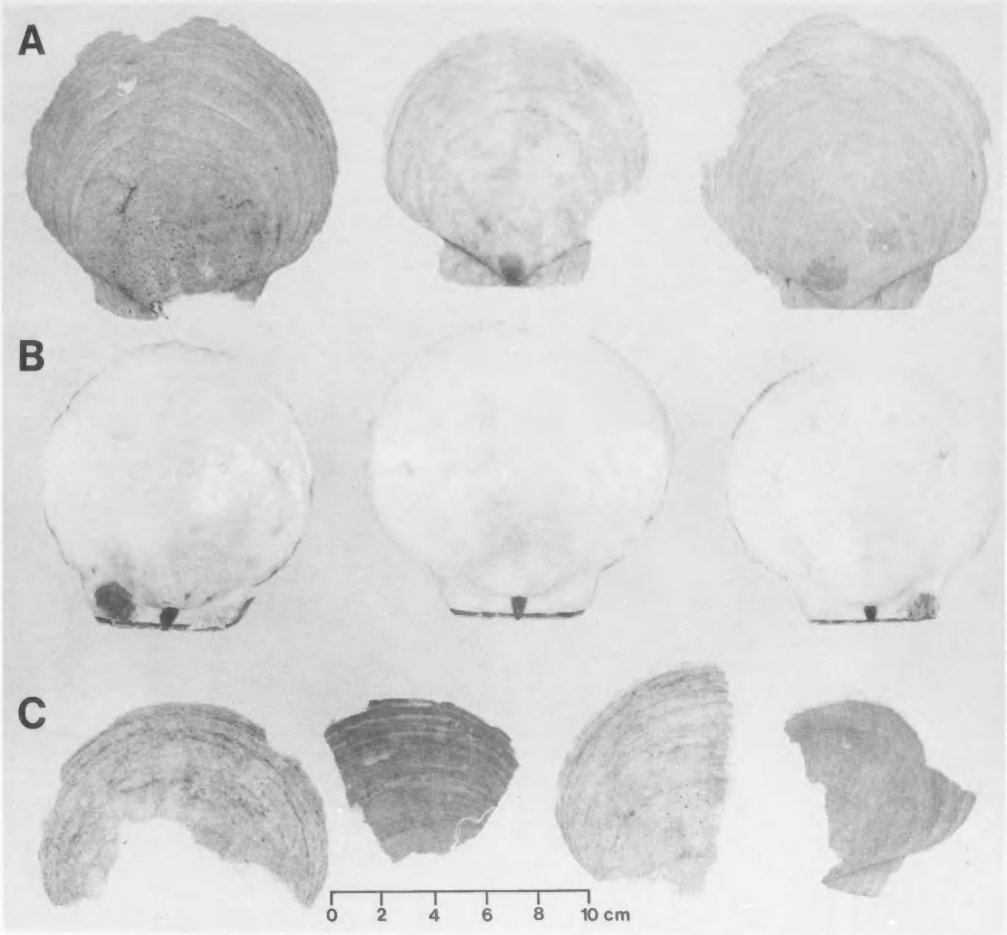

FIG. 2. The top valve remains of the 10 scallops eaten by lobsters. (A) Edges chipped; (B) remanents of the bottom valve still attached to the top valve; (C) complete fragmentation.

predator–prey size was important in determining predation rate. For the size ranges of lobster and rock crab used, preferred prey scallop heights are estimated to be around 30–50 mm, much less than the average 90- to 100-mm height of large scallops used in both these studies.

Why large scallops sometimes rank lower than large horse mussels in the diets of both predator species is not immediately obvious. Although the nutritional value of both horse mussels and scallops may differ, the difference between the two species is hypothesized to be vulnerability to predation. On a hard substrate, Breen (1974) observed a low lobster predation rate on loose horse mussels, as did we in 1980, whereas in the 1979 study the mussels were embedded in the substrate and were readily consumed. The mussel sizes presented to lobsters by Breen (1974) averaged 66 mm in length, considerably less than the average mussel size of 83 mm available to the lobsters in both our studies. Large mussel predation by lobsters may thus be facilitated if the mussels are embedded in the substrate rather than being loose upon it. Scallops, in contrast, do not embed and can move, and although large scallops seldom escape by swimming (Caddy 1968), escape behavior may nevertheless impede successful attack.

In laboratory studies, small scallops have been crushed in the lateral plane by the large chelae of lobsters. Lobsters were frequently observed biting away at the margins of large scallop valves, but this latter technique was relatively unsuccessful as an opening technique (Elner and Jamieson 1979). The shell remains of large scallops found in the corrals showed evidence of biting and crushing (Fig. 2), and because scallops were ultimately opened, we suggest that the low predation rate by lobsters on large scallops results from handling difficulties encountered by the lobsters.

Green crabs can successfully open blue mussels (*Mytilus*

edulis) whose shells' compressive strength approximates that of the strength of the crab's chelae, and Elner (1978) postulated that this was the result of the crab's seeking out and exploiting by trial and error weak spots in the mussel's shell. Eventual shell breakage was the result of a cumulative process of extending minute fractures in the shell substructure. At high lobster densities, lobster interference with each other might provide insufficient opportunity for prey manipulation and exploitation of shell weaknesses. Only when predator density was low and the lobsters were hungry enough to justify the increased handling cost (Elner and Hughes 1978) could large scallop predation occur.

The absence of rock crab predation of recruited scallops in 1979 could have resulted from a number of factors: crab density may have been too high, resulting in crab interference with each other; the scallops may have been too large to be grasped adequately by a crab's relatively small chelae; or crab chelae strength may have been insufficient to crush the valves.

Predation of both small and large scallops by rock crabs occurred in the 1980 study. Crab density was lower than in the 1979 study, and this supports the hypothesis of an interference effect during predation at very high predator densities. However, differences in environmental conditions in the 2 yr as a cause for differences in predation have not been ruled out.

Decapod predation may represent a significant component of the natural mortality of small scallops, as well as being a factor in the natural and indirect fishing mortalities of large scallops. Nonlethally injured, large scallops damaged during dragging may be more vulnerable than undamaged scallops, and because predators are known to be attracted to the drag path of a dredge (Caddy 1973), such scallops may be preyed upon at a higher rate than shown in this study.

Because large scallops are not apparently preferred prey for decapods, the use of "cluckers" (empty scallop valves still attached by the hinge) appears acceptable as a means to estimate large scallop natural mortality (Dickie 1955; Merrill and Posgay 1964) in areas where decapods occur. Because decapods invariably separate the valves, significant predation, if it occurred, would result in an underestimation of natural mortality if it was determined by clucker abundance alone. For small scallops, caution should be taken in estimating their natural mortality from "clucker" abundance as the natural predation rate of small scallops by decapods appears greater.

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Application of X-ray Microanalysis for the Detection of Heavy Metals in Great Lakes Algae

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A combination of scanning electron miscroscopy and energy dispersive X-ray spectroscopy (SEM-EDX) was found to be a very effective tool for characterizing the heavy metal load of Great Lakes phytoflagellates, diatoms, and green algae, and for the surveillance of heavy metal pollution. The sensitivity and short generation time of nannoplankton and the speed of the described technique makes this procedure a useful aid in contaminants research.

Key words: scanning electron microscopy, X-ray microanalysis, nannoplankton, heavy metals, algae, phytoflagellates, Great Lakes, contaminants, bioaccumulation

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On a constaté qu'une combinaison de la microscopie électronique à balayage et de la spectroscopie à rayons-X dispersifs d'énergie (SEM-EDX) était un outil efficace avec lequel caractériser la charge en métaux lourds des phytoflagellés, des diatomées et des algues vertes des Grands Lacs, et surveiller la pollution par métaux lourds. À cause de la sensibilité et du court intervalle entre générations du nannoplancton et de la rapidité de cette methode, elle est un instrument utile de recherche sur les contaminants.

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DUE to the growing concern about the levels of various contaminants and heavy metals in the Great Lakes, a considerable amount of experimental research has been carried out to study the effects of contaminants on laboratory-grown cultures. Very little is known, however, about the occurrence of heavy metals which might have accumulated in various species of algae as a result of metabolic processes under natural conditions (Healey 1973). The wet chemistry methods currently used to detect the presence of heavy metals in phytoplankton require large samples and make such an operation expensive, cumbersome, and time consuming. Therefore, we attempted to elaborate further the recently developed morphological routine for scanning electron microscopy and combine it with X-ray microanalysis (Fitzgerald et al. 1968) to allow rapid detection of heavy metal pollution for surveillance purposes.

Methods and materials — Phytoplankton samples, fresh or preserved in Lugol's solution, were prepared according to a procedure described previously (Bistricki and Munawar 1978). The procedure allows rapid preservation of delicate phytoflagellates and prolonged storage of samples for subsequent morphological and microanalytical studies (Munawar

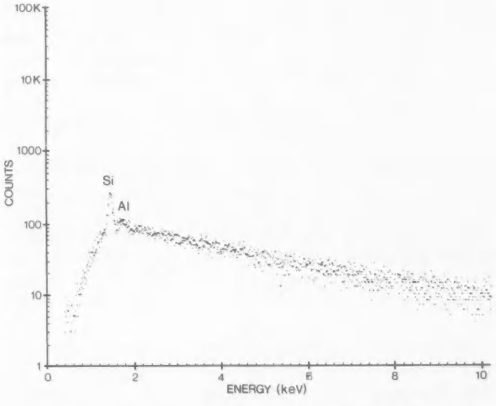

FIG. 1. A background spectrum obtained under conditions identical with those used in other measurements taken from the area of the specimen containing no structures of interest.

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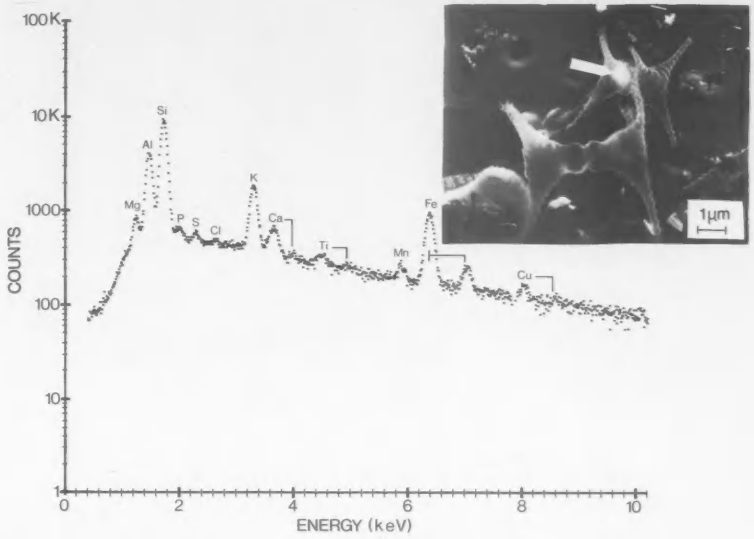

FIG. 2. Air-dried specimen of *Staurastrum paradoxum* (magnified 9000×) and an X-ray spectrum showing elemental composition at the location indicated by the arrow.

and Bistricki 1979).

Aliquots of the samples were filtered through Nuclepore membranes of 0.45-μm porosity, washed with purified 0.05 mol/L S−collidine buffer which contained no traces of heavy metals (Polysciences, Warrington, PA), and fixed with a solution of osmium tetroxide prepared in the above buffer. After being washed and dehydrated in alcohol the filtered specimens were dried by the critical point drying technique.

The membrane filters were mounted on a specimen support stub and transferred into a vacuum evaporator. A 20-nm layer of carbon was evaporated on the surface of the specimens to facilitate thermal and electrical conductivity.

The examination of material was done by an AMR 1000 electron microscope equipped with an energy dispersive X-ray spectrometer and a computer-based data processing system (Tracor-Northern, TN-11).

Material was sampled at several locations in Lakes Superior, Ontario, and Erie during the spring and summer months of 1980. Thirty samples were processed and analyzed for the heavy metals content. Each specimen was systematically scanned in the zig-zag pattern across the surface of the stub at a convenient magnification (1000 to 2000 times depending on the size of phytoplankter under examination). Elemental spectra were obtained from several locations on the cell surface. The electron beam was kept stationary on the chosen spot for 120 or 180 s. Also, background spectra were obtained under conditions identical with those used in other measurements. These readings were taken from the area of the specimen which did not contain any structures of interest (Fig. 1). Such a background excludes the possibility of spurious instrumental signals being present in the analyses. The spectra were recorded on a digital storage device for future reference. A total of 120 organisms of various species were examined. Three typical examples from different environments were chosen to demonstrate the application of this procedure.

Results and discussions — Figure 2 shows *Staurastrum paradoxum*, a commonly occurring green alga in the eutrophic waters of western Lake Erie (Munawar and Munawar 1976). The elemental spectrum demonstrates the presence of metals in a cellular structure. Besides Mn and Cu, elevated levels of Fe and Al were detected. Other elements indicated in the spectrum are inherent structural components found in biota under normal conditions.

Figure 3 exhibits a nannoplanktonic species of *Cyclotella* from Lake Superior found usually in oligotrophic waters. The elemental spectrum surprisingly shows the presence of Cu, although the ambient concentration of copper in the water was at a very low level (2 μg/L). This spectrum also shows a group of iodine peaks at the 3.940-keV level generated by the preservative medium and several peaks from naturally occurring elements.

Figure 4 shows *Rhodomonas minuta*, a delicate cryptomonad phytoflagellate from Lake Ontario found in waters of varying trophic levels. The elemental spectrum is vertically expanded to show small peaks at 10.550, 12.630, and 14.770 keV corresponding to X-ray energy of Pb (L) lines. Small peaks of Fe and Cu and a group of osmium peaks interlaced with Cu and Pb signals are also evident in the spectrum.

These results confirm the previously indicated possibility that certain nannoplanktonic species, because of their sensitivity and short generation time, can be used as indicators of

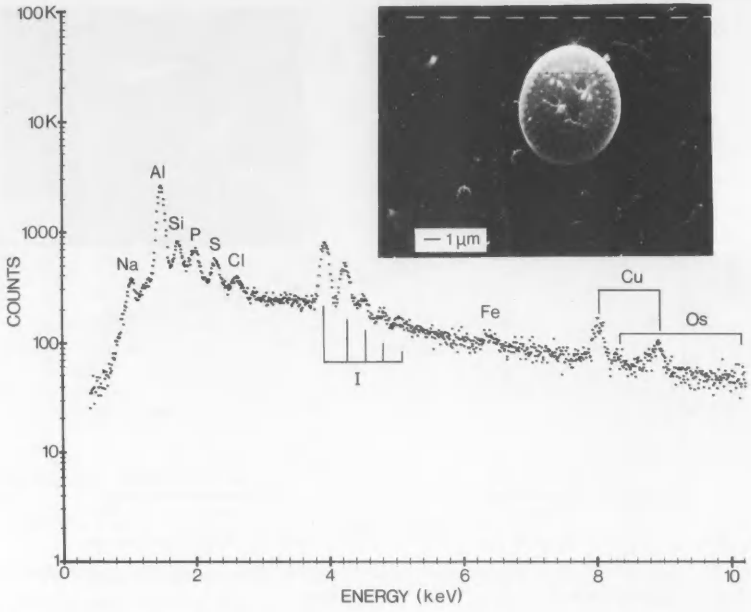

FIG. 3. Lugol-preserved specimen of *Cyclotella* sp. (magnified 5000×) along with an X-ray spectrum showing elemental composition obtained from the above cell.

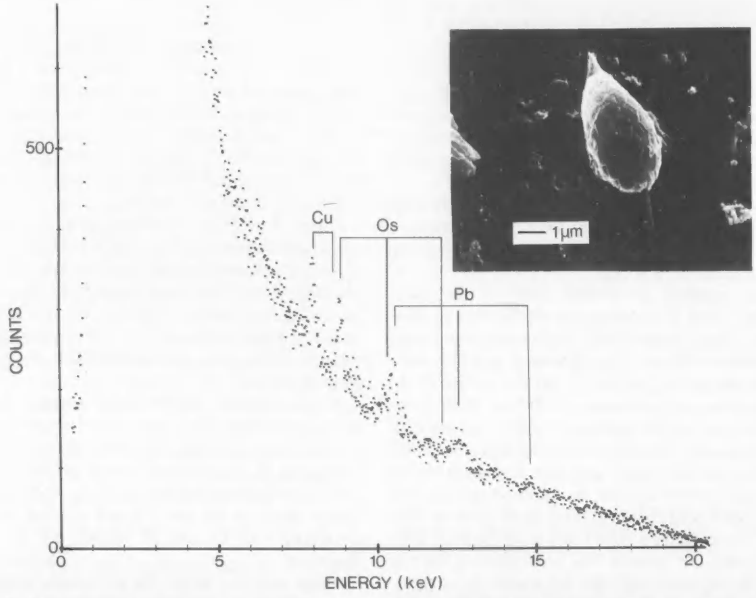

FIG. 4. Lugol-preserved specimen of *Rhodomonas minuta* (magnified 9000×) and the X-ray spectrum from the dorsal central region of the cell.

heavy metal pollution (Munawar and Bistricki 1979). It was also determined that very low levels of metals in ambient waters can be bioaccumulated to a relatively high concentration in phytoflagellates, diatoms, and green algae.

The described procedure permits the identification of affected species in a natural and mixed population. Such an approach makes it possible to undertake the surveillance of heavy metals in phytoplankton species which, being the primary producers, are affected first. This kind of an early warning system in surveillance operations should not be ignored because it allows detection of heavy metals before these are transferred through the food chain to fish. At such a level the analytical procedures become more expensive and delay the evaluation of surveillance results.

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Decreased Seawater Adaptability of Chum Salmon (*Oncorhynchus keta*) Fry Following Prolonged Rearing in Freshwater

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Chum salmon (*Oncorhynchus keta*) fry weighing about 1 g maintained plasma Na^+ concentrations at 134–140 mmol/L during seaward migration in the Otsuchi River. The plasma Na^+ level increased slightly in the estuary, and reached 150–160 mmol/L in the fry caught in the bay. On direct transfer from freshwater to seawater, the plasma Na^+ concentrations of the fry weighing 0.4–2.3 g increased markedly after 1 h and reached a maximum after 3–12 h. The fry of <1.4 g attained seawater-acclimated plasma Na^+ level of 156 mmol/L within 24 h after transfer, whereas fry of 1.8–2.3 g failed to adapt to seawater within 24 h. When seawater adaptability of fry of different lots was examined simultaneously in late April, 83–109 d after hatch, the smaller fry adjusted their plasma Na^+ levels more easily than the larger fry: the smallest fry attained seawater level after 12 h without showing any peak. Changes in seawater adaptability of the same lots of fry were also followed until 5 mo after hatching, and the osmoregulatory ability of the fry in seawater decreased gradually with an increase in body weight or in the time spent in freshwater.

Key words: chum salmon fry, seaward migration, plasma Na^+ concentration, seawater adaptability, *Oncorhynchus keta*

IWATA, M., S. HASEGAWA, AND T. HIRANO. 1982. Decreased seawater adaptability of chum salmon (*Oncorhynchus keta*) fry following prolonged rearing in freshwater. Can. J. Fish. Aquat. Sci. 39: 509–514.

Des alevins de saumon keta (*Oncorhynchus keta*) pesant environ 1 g maintiennent leur concentration de Na^+ plasmatique à 134–140 mmol/L lors de leur migration vers la mer dans

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le fleuve Otsuchi. Le niveau de Na^+ plasmatique augmente légèrement dans l'estuaire et atteint 150−160 mmol/L chez les alevins capturés dans la baie. Quand des alevins pesant 0,4−2,3 g sont transférés directement de l'eau douce à l'eau de mer, les concentrations de Na^+ plasmatique augmentent notablement après 1 h et atteignent un maximum après 3−12 h. Les alevins de moins de 1,4 g atteignent le niveau de Na^+ plasmatique d'acclimatation à l'eau de mer de 156 mmol/L en moins de 24 h après le transfert tandis que les alevins de 1,8−2,3 g ne s'acclimatent pas à l'eau de mer en dedans de 24 h. À l'examen simultané de l'adaptabilité à l'eau de mer d'alevins de différents lots à la fin d'avril, 83−109 jours après éclosion, on constate que les petits alevins règlent leur niveau de Na^+ plasmatique plus facilement que les grands. Les plus petits alevins atteignent le niveau d'acclimatation à l'eau de mer en 12 h, sans aucun pic. On a de plus suivi les changements d'adaptabilité à l'eau de mer des mêmes lots d'alevins jusqu'à 5 mois après éclosion. La capacité osmorégulatrice des alevins en eau de mer diminue graduellement à mesure qu'augmente le poids corporel ou la durée du séjour en eau douce.

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AMONG the Pacific salmon (genus *Oncorhynchus*), chum (*O. keta*) and pink salmon (*O. gorbuscha*) are unique in the ecology of their early life stages. They spawn close to the sea, and the young return to the sea as fry soon after yolk absorption. This is in contrast to the upstream spawning location of chinook (*O. tschawytscha*) and sockeye (*O. nerka*) and the longer freshwater residency of chinook, sockeye, coho (*O. kisutch*), and masu (*O. masou*) fry (Tyler and Bevan 1964; Hoar 1976; Kobayashi and Abe 1977). According to Kashiwagi and Sato (1969), seawater adaptability of chum develops gradually throughout the alevin period: more than 80% of alevins on days 1, 10, and 20 after hatching, survived well in 25, 50, and 75% seawater, respectively. Weisbart (1968) compared seawater adaptability of embryos, alevins, and fry of five species of Pacific salmon by transferring them directly to seawater. Although the high salinity of seawater was lethal to all the embryos (2 wk before hatching) and alevins (2 wk after hatching), chum and pink embryos, and alevins showed significantly greater salinity resistance than those of coho, chinook, and sockeye. Chum and pink fry (5 mo after hatching) adapted well to seawater, whereas fry of other species failed to survive.

In recent years in Japan, in order to increase the returning population of chum salmon, all ascending mature fish are collected for artificial propagation. The fry are reared in the hatchery until they grow to 1−3 g in body weight or until at least 1 mo after hatching, before they are released into the rivers. Prolonged rearing in the hatchery is recommended, mainly based on the observation by Hiyama et al. (1972) that larger fry evade natural predators such as rainbow trout and gobies better than smaller fry. However, there is no information on changes in seawater adaptability of the chum fry reared in the hatchery. This investigation was carried out to study the relationship between seawater adaptability of the fry, and their size or time spent in freshwater. Thus, changes in plasma sodium concentrations were followed during the migration of chum fry from freshwater to seawater, and their migratory behavior was related to the changes in their seawater adaptability.

Materials and methods — The Otsuchi Salmon Hatchery is located 1.7 km upstream on the Otsuchi River. Mature chum are caught 500 m upstream from the river mouth from mid-November to mid-December for artificial fertilization. About 25 million eggs were incubated in running water (12.5°C), supplied by two wells. The embryos hatched in late January or early February. The water from the hatchery forms the Gensui Creek (500 m long), which joins the Otsuchi River, 1.2 km upstream from the mouth of the river. From late March to April the fry are released into the Otsuchi River at the junction with the Gensui Creek. The water temperature at the time of release was 11.0−11.3°C in the Gensui Creek and 6−9°C in the Otsuchi River.

The fry released from the Otsuchi Salmon Hatchery on April 19, 1979 (mean body weight, 1.03 g; mean fork length, 53 mm; on a complete diet of commercially prepared fish pellets for 24 d) were sampled at various points along the Otsuchi River and in the estuary. More than 10 fry in each sample were transported in plastic bags containing oxygen-saturated water (10 L) from the collection spots. The fish seemed to be under handling stress immediately after transportation from river to laboratory, and plasma Na^+ concentration was variable. Therefore, the fry were kept at 10°C in the same water for 24 h before collection of blood samples.

During April 1979, three groups of fry weighing 0.3−1.3 g were transferred from the School of Fisheries Science, Kitasato University (sample A), and from the Otsuchi Salmon Hatchery (samples B and C) to the Otsuchi Marine Research Center. The fry of groups A and B hatched between January 28 and February 5, and those of group C, between January 4 and 7, 1979. The fry of group A were smaller than those of group B, although both groups had hatched at about the same time. The difference in their growth rates was attributable to the difference in rearing temperature at Kitasato University (6°C) and at Otsuchi Hatchery (12.5°C). All of the fry were reared in freshwater tanks (1000 L, 10°C) for various periods until July 1979, under normal spring and summer light conditions in the laboratory. An artificial diet (Masu No. 2, Nihon Nosan Kogyo) was supplied twice daily. Growth was good, and mortality was less than 2% in total during the experimental period.

In order to evaluate the ability of the fry to regulate their plasma ion levels in seawater, the time course of changes in plasma Na^+ levels was followed after direct transfer from freshwater to seawater (10°C, 33.5‰ in salinity). Plasma samples were taken from 15 to 20 fish after 1, 3, 6, 12, 24,

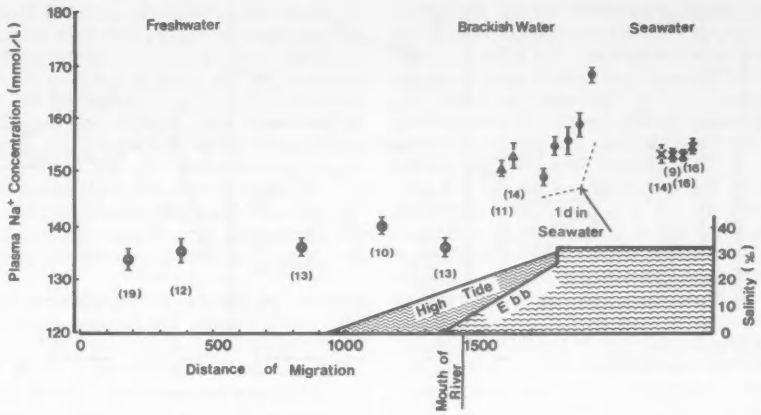

FIG. 1. Plasma Na^+ concentrations of chum salmon fry caught in the river (○), estuary (△), and bay (X), and of fry 24 h after transfer from freshwater to seawater (●). Vertical bars represent standard errors. (Numbers of fry are in parentheses.) Salinity is shown at bottom right.

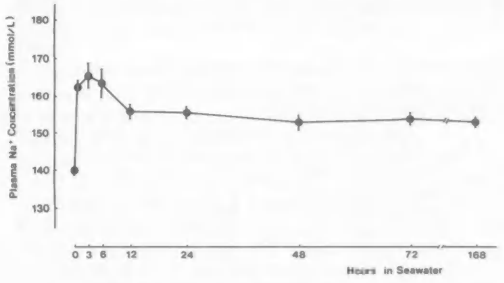

FIG. 2. Changes in plasma Na^+ concentrations of chum salmon fry (mean body weight, 0.74 g) after transfer from freshwater to seawater. Plasma samples were taken from 15 to 20 fish at each point. Vertical bars represent standard errors.

48, and 72 h, and 1 wk. Because seawater adaptation of the chum fry weighing about 0.7 g was completed within 24 h after seawater transfer, the seawater adaptability of fry of various sizes and of fry reared in freshwater for different periods of time was then evaluated by determining changes in plasma Na^+ levels after 3, 12, and 24 h in seawater. Seawater adaptability of fry of different lots (groups A, B, and C) was examined simultaneously in late April. All fry were held in freshwater for at least 2 wk before the first experiment.

Blood was collected from the caudal artery following the procedure developed by Jozuka and Adachi (1979). Each fry was quickly dried on paper toweling, positioned lateral side up on a paraffin sheet with tape, and an incision made in the skin slightly behind the anus. After the skin was peeled off with fine forceps, one side of the caudal musculature was removed with a razor blade, to expose the caudal artery and vein. About 5 μL of blood was taken from the caudal artery with a fine-tipped capillary tube (made of Drummond, precision disposable micropicette, 20 μL), using a dissection microscope. The capillary tube of blood was sealed (Sealease, Clay-Adams), and the plasma separated by centrifuging at 10 000 rpm for 10 min at room temperature. Sodium concentration of the plasma was measured by atomic absorption spectrophotometer (Hitachi 170-50 or Hitachi 203) after 1000 times dilution with deionized water. Data are presented as means ± SE. Multiple non-independent comparison (Dunnett's procedure) was applied to compare the means with a control.

Results — The means of plasma Na^+ concentration of the fry sampled from the river were 134−140 mmol/L (see Fig. 1), and there was no significant difference among five shoals regardless of migration distance from the releasing point. The fry were also caught in the estuary 24 h after release, and the plasma Na^+ concentration (151, 153 mmol/L) was significantly higher ($P < 0.01$) than that in the river, almost the same as in the fry adapted to seawater.

Plasma Na^+ concentration in fry (Fig. 2) increased significantly ($P < 0.01$) from 140 mmol/L in freshwater to 163 mmol/L after 1 h in seawater, and reached a peak at 3 h (166 mmol/L). The plasma Na^+ level was high at 6 h, but decreased to the seawater-acclimated level of 155 mmol/L after 12−24 h. There was no mortality during the experiment.

As shown in Fig. 3A and Table 1, plasma Na^+ concentration of the smallest fry (group A-1, body weight, 0.41 g) increased from 136 mmol/L in freshwater to 145 mmol/L after 3 h in seawater and to 154 mmol/L after 12 h. They attained the seawater-acclimated level within 12 h without showing any sharp peak, although there was a tendency toward a decrease after 24 h. In this group, a small quantity of yolk still remained in some of the fry. Fry of similar stages are known to start seaward migration in nature. The plasma Na^+ concentrations of groups B and C-1 at 0 h were larger than that of group A-1 by 5−11 mmol/L. Fry weighing 0.74 g (group B) showed maximal Na^+ level 3 h after transfer, but attained the seawater level after 12−24 h. Plasma Na^+ concentration of the large group (group C-1) weighing 1.26 g similarly reached a peak after 3 h. However, the levels after 12-24 h were still

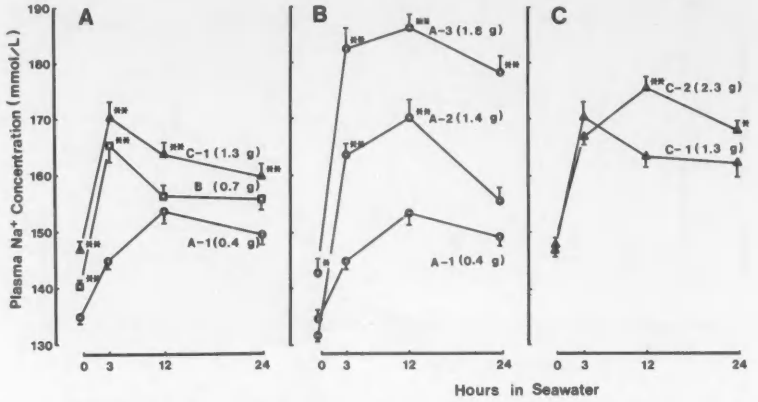

FIG. 3. Changes in plasma Na^+ concentrations of various groups of chum salmon fry after direct transfer from freshwater to seawater. (A) Seawater adaptability of fry of different lots (groups A-1, B, and C-1) examined simultaneously in late April. (B and C) Changes in seawater adaptability of the same lots of fry (groups A-1, -2, -3, and C-1, -2) following prolonged rearing in freshwater. Plasma samples were taken from 12 to 16 fish at each point. Vertical bars represent standard errors. Significantly (* $P < 0.05$; ** $P < 0.01$) different from the level in group A-1 fish and from that in group C-1 fish. See Table 1 for duration reared in freshwater.

TABLE 1. Changes in plasma Na^+ concentration of various sizes of chum salmon fry after direct transfer into seawater.

Group	Day after hatching	Body weight (*g*) Mean ± SE (*N*)	Plasma Na^+ concentration (mmol/L) Initial	Maximum	% Change	Mortality at 24 h (%)
A-1	83	0.41±0.08 (59)	136±1.2 (16)	154±2.5 (14), 12 h[a]	13.2	0
B	83	0.74±0.25 (58)	140±1.1 (15)	166±3.2 (14), 3 h	17.7	0
C-1	109	1.26±0.25 (55)	147±1.4 (13)	170±2.8 (14), 3 h	15.6	0
A-2	129	1.43±0.24 (56)	132±1.0 (13)	171±3.5 (14), 12 h	29.5	6.3
C-2	140	2.25±0.37 (51)	148±1.1 (12)	176±1.9 (13), 12 h	18.9	11.8
A-3	157	1.76±0.38 (57)	144±2.3 (15)	187±2.8 (14), 12 h	29.9	29.4

[a]Time after transfer to seawater when maximal level occurred.

high as compared with those of group A-1 ($P < 0.01$).

In the next experiment, changes in seawater adaptability of the same lots of fry (groups A and C) were examined from April to July (Fig. 3B and C, and Table 1). When the fry of group A were reared for about 2 mo and weighed 1.43 g (group A-2), the maximum increase in Na^+ level had decreased to 156 mmol/L. The fry of this group attained the seawater-acclimated level within 24 h. Plasma Na^+ concentration of the fry in group A-3 (body weight, 1.76 g), reared in freshwater for the longest period (6 mo after hatch), reached 183 mmol/L after 3 h and still remained high after 24 h. About 30% of the fry of this group died within 24 h after transfer to seawater (Fig. 3B). The same tendency was observed in the fry of group C (Fig. 3C). The growth rate of this group was still better than that of group A. In the largest fry of this group (group C-2) weighing 2.25 g, maximal concentration (176 mmol/L) occurred after 12 h and was maintained after 24 h. The levels were significantly higher ($P < 0.01$ at 12 h and $P < 0.05$ at 24 h) than in C-1 fish.

As also shown in Table 1, plasma Na^+ concentration of the fry in freshwater increased in parallel with an increase in their body weight. The maximal levels reached, 3–12 h after transfer to seawater, were also greater in larger fry than in the smaller fish. Correlation between plasma Na^+ levels in freshwater (Y_1) and body weight (X) can be expressed as $Y_1 = 6.1X + 133$ ($r = 0.604$, $P < 0.01$), and that between the maximal levels in seawater (Y_2) and body weight (X) as $Y_2 = 12.7X + 154$ ($r = 0.615$, $P < 0.01$). These results also indicate that smaller fry or fry with a shorter time in freshwater are able to adapt to seawater more efficiently than larger fish.

Discussion — In Japan, the chum salmon *Oncorhynchus keta* is especially abundant in the waters of Hokkaido and the northern part of Honshu. In the Sanriku area, where the Otsuchi Marine Research Center is located, mature fish return to their natal river during October–January. Artificial propagation of the chum is common in this area. Eggs are fertilized artificially and reared in the hatchery until they attain an average body weight greater than 1 g. The fry weighing 0.5–2.5 g are released into the river from March to May. In the present study, chum fry weighing about 1 g maintained plasma Na^+ concentrations at 134–140 mmol/L during their seaward migration, throughout a distance of 1.7 km in the Gensui Creek and the Otsuchi River.

At the lower reaches of the Otsuchi River, salinity fluctu-

ates with changes in tidal level. The saline wedge reaches 700 m upstream from the river mouth at high tide, but less than 200 m at low tide. Salinity of the bottom layer of the estuary is about 32−33.5‰ regardless of tidal condition, but that of the surface layer changes rapidly from 2 to 25‰ throughout the estuary. During seaward migration, chum fry were always found in the upper, low salinity layer of the estuary (Iwata unpublished observation). The Na^+ concentration of the fry caught within 24 h after release was about 152 mmol/L in the brackish area, which was almost the same as in seawater-adapted fry. They seem to begin to adjust their plasma Na^+ concentration to the seawater level in the brackish water at the estuary.

Chum and pink salmon acquire salinity tolerance earlier in life as compared with other salmonid species (Parry 1960; Conte and Wagner 1965; Conte et al. 1966; Weisbart 1968; Kashiwagi and Sato 1969; Kobayashi and Harada 1966). When transferred directly to seawater, the chum fry was able to adjust plasma ion levels within 24 h. The quick adaptation of the chum and pink fry to seawater has also been reported earlier (Black 1951; Parry 1960; Houston 1961; Weisbart 1968). The osmoregulatory capability is related to the effects of temperature, photoperiod, and stages of parr−smolt transformation (Adams et al. 1973; Wagner 1974; Zaugg and Wagner 1973; Zaugg and McLain 1976; Ewing et al. 1979, 1980).

It has also been generally accepted that salmonids exhibit a sharp increase in salinity tolerance as the young fish increase in size, and that for a given age, the larger fish are more resistant (Ewing et al. 1980; Wagner et al. 1969). Using a stock of chum from British Columbia, Houston (1961) reported that 1.6-g fry were better able to regulate total body chloride levels after transfer to seawater than were 0.9-g fry. This is in contrast with the present findings that, when the seawater adaptability of chum fry was examined by following the changes in the plasma Na^+ levels, smaller fry or fry with shorter time in freshwater adapted to seawater more efficiently than the larger fish.

This difference is unlikely to be due to the different methods used to examine the seawater adaptability — changes in total body Cl^- by Houston and in plasma Na^+ by us. Chum fry were kept in the laboratory aquarium at 10°C for more than 2 wk before transfer to seawater (10°C, 33.5‰). When fry of different lots were transferred to seawater simultaneously in late April, the smaller fry could regulate the plasma Na^+ concentration at a lower level better than the larger fry throughout 24 h. When the seawater adaptability of the same lot of the fry were followed until 5 mo after hatching, there was a tendency toward an increase of plasma Na^+ level of the fry maintained in freshwater after April. Therefore, the osmoregulatory ability of the fry in seawater decreased gradually with an increase in body weight or in time spent in freshwater. Houston (1961) carried out his experiments from May to July, and the fish were transferred to seawater (10°C, 22−24‰) after being kept in freshwater (10−16°C) for 35−40 h. Although no further information is available whether his 0.9- and 1.6-g fry were from the same lot or whether they were transferred to seawater simultaneously or at different timings, the difference between Houston's findings and ours could be due to rearing conditions and growth rate in freshwater, or to the timing of seawater transfer. It may also be possible that the difference is due to genetic difference between the Japanese and Canadian stocks of fry.

In most salmonids, an increase in seawater tolerance is observed during spring time, generally in association with parr−smolt transformation, and the seawater tolerance regresses when the fish are retained in freshwater (see Hoar 1976). But plasma Na^+ concentrations of our fry maintained in freshwater increased in parallel with an increase in size. This may be a size-related phenomenon which accompanies the growth of fishes. At any rate, the decreased seawater adaptability of the chum fry in parallel with an increase in body weight or in time spent in freshwater may be comparable to the loss of seawater adaptability or preference observed in postsmolt fish of the other salmonids. However, early fry of chum are silvery, although they still have parr marks. During the prolonged rearing in freshwater, the parr marks disappear and the fish resemble smolts. Moreover, it is difficult to maintain the chum fry for more than a year in freshwater (Kubo 1953; Baggerman 1960). Some of our large-sized fry reared in freshwater for more than 5 mo (group A-3) were unhealthy, and 30% of them died in seawater within 24 h. According to Baggerman (1960) and McInerney (1964), chum fry exhibited consistent seawater preference for several months until all fish died by November. Therefore, early development of seawater adaptability and a subsequent loss of freshwater adaptability as observed in the chum fry seem to be induced or controlled by mechanisms, which are different from those in other salmonids.

Hiyama et al. (1972) reported that the large-sized chum fry evade natural predators in the river during seaward migration, and suggested that prolonged rearing in the hatchery will result in an increase in returning population of the mature fish. Chum lose both freshwater and seawater adaptability during prolonged rearing in freshwater in this study, while maintaining seawater preference (Baggerman 1960; McInerney 1964). The freshwater adaptability seems to develop again in the adult fish during spawning or homing migration (Hirano et al. 1978; Morisawa et al. 1979). Therefore, to keep fry in a hatchery for longer periods to make them larger may not necessarily be advantageous for their smooth adaptation to seawater.

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Influence of Age, Size, and Temperature on Metamorphosis in the Starry Flounder, *Platichthys stellatus*

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POLICANSKY, D. 1982. Influence of age, size, and temperature on metamorphosis in the starry flounder, *Platichthys stellatus*. Can. J. Fish. Aquat. Sci. 39: 514–517.

The onset of metamorphosis of starry flounders (*Platichthys stellatus*) reared at the New England Aquarium was more strongly related to size than to age. For three of the eight crosses the regression of standard lengths (SL) of the progenies at metamorphosis on age was not different from 0 at the 10% significance level. For the other five the regression coefficients

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were negative and different from 0 at the 5% level but only 11.2% or less of the variation in SL at metamorphosis was accounted for by age. Progeny from one of the crosses were reared at two temperatures; at the higher temperature the time to metamorphosis was greatly reduced, but there was only a small change in the SL at metamorphosis.

Key words: metamorphosis, age, size, development, demography, temperature, starry flounder

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Le déclenchement de la métamorphose chez la plie du Pacifique (*Platichthys stellatus*) élevée à l'Aquarium de la Nouvelle-Angleterre est reliée davantage à la taille qu'à l'âge. Dans le cas de trois sur huit croisements, la régression des longueurs standard (LS) des descendants à la métamorphose sur l'âge ne diffère pas de 0 au niveau de signification de 10 %. Dans les cinq autres cas, les coefficients de régression sont négatifs et diffèrent de 0 au niveau de 5 %, mais l'âge ne peut expliquer que 11,2 % ou moins de la variation de LS à la métamorphose. Les descendants d'un des croisements furent élevés à deux températures; à la température la plus haute, la période d'avant-métamorphose fut considérablement réduite, mais il n'y eut qu'un faible changement de LS à la métamorphose.

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MANY teleosts undergo a marked change in morphology and physiology fairly early in development. This metamorphosis, a complex process involving growth and differentiation, is an important aspect of the life history. There is an enormous literature on the influence of temperature on the rate of development of eggs and yolk-sac larvae, and on the growth rate of older fish (Blaxter 1969; Brett 1979; Miller 1979), and some discussion of the influences of temperature, age, and size on metamorphosis in other ectotherms (Etkin 1964; Howe 1967; Lock and McClaren 1970; Smith-Gill and Berven 1979). But, perhaps due to the difficulty of rearing fish, information is sparse on the influence of environmental variables on metamorphosis.

In this paper I present results of experiments to determine the influences of age, size, and temperature on metamorphosis in the starry flounder, *Platichthys stellatus*.

Materials and methods — Adult starry flounder collected in Monterey and San Francisco Bays, Puget Sound, and Japan were induced to become ripe by means of hormone injections. Eggs were selected, artificially fertilized, and hatching larvae were reared at the New England Aquarium as described by Policansky and Sieswerda (1979). Following preliminary experiments (1977, 1980), I made eight crosses involving five males and three females in 1981. The fertilized eggs from each cross were placed in individual 19-L tanks, held in four water baths at different, somewhat variable temperatures (Table 1). The temperature in each bath was recorded once or twice each day until all the fish had completed metamorphosis. I checked all the tanks for visible signs of metamorphosis (eye migration) daily until the first fish metamorphosed; thereafter every metamorphosing fish was removed and measured daily, and returned to a previously unoccupied tank, or preserved. I measured the standard length (SL) of metamorphosing fish from the various tanks to the nearest 0.1 mm using an ocular micrometer in a dissecting microscope. Although I attempted to remove all fish in the earliest metamorphic stage, a few were measured on one of the following 2 d. Because the process of eye migration is extremely rapid, taking about 6 d, and is not accompanied by an increase in length, only small inaccuracies were thus introduced.

All tanks were initially stocked with several thousand fertilized eggs. In those tanks with good hatching and larval survival, I culled individuals after about 2 wk to reduce the density to about 100 larvae per litre. One pair of fish was still ripe 14 wk after the initial fertilization, and that cross was repeated. By this time of year (April 12) the water begins to warm up in the Aquarium; thus I was able to rear fish of the same genotype at different temperatures.

Results — The earliest fish initiated metamorphosis at 27 d (in 1977) and the latest at 104 d (1981). The mean times to metamorphosis in 1981 varied from 39.3 to 75.3 d (Table 1).

At metamorphosis the smallest fish, not from one of the eight crosses analyzed, was 4.8 mm SL and the largest fish 9.0 mm SL. Mean size at metamorphosis in 1981 ranged from 6.6 to 7.7 mm SL (Table 1).

Although in five of eight crosses there was a significant negative relationship between size (SL) and age of progeny at metamorphosis (Table 1), only 11.2% or less of the variation in SL was accounted for by age. To indicate the distribution of points, the results of the cross with the strongest relationship (91 × 98) and the results of a cross with no relationship (82 × 59) are plotted in Fig. 1 and 2. When progeny of a cross (82 × 98) were raised at two temperatures (Table 1), at the higher temperature there was a marked reduction in the age at metamorphosis (*t*-test, $P < 0.0001$) and a slight but statistically significant increase in the SL ($P < 0.005$) (Fig. 3). The regression coefficient is similar to those of several of the other crosses in which the progeny were reared at only one temperature (Table 1). It is thus impossible to separate the influences of temperature on size and age. The difference between the two temperatures (Table 1) was significant (*t*-test, $P < 0.0001$). These results indicate that metamorphosis was much more strongly influenced by size than by age.

TABLE 1. Relationships between age and SL at metamorphosis of starry flounder (*Platichthys stellatus*) from various crosses. Individual fish are identified by numbers. Means are given ± standard deviations. Mean temperatures are from day of fertilization to last metamorphosis for each tank. Differences in age of at least 4 d and differences in SL of at least 0.15 mm are significant at the 0.01 level.

Parents (♀ × ♂)	Mean temp. (°C)	Mean age (d)	Mean SL (mm)	Regression coefficient	r	N	P(slope = 0)
91 × 59[a]	10.61±0.81	66.3±8.85	7.43±0.44	−0.0062	−0.127	487	<0.01
91 × 87	10.61±0.81	67.4±9.93	6.79±0.35	−0.0068	−0.192	127	<0.05
91 × 89	10.51±0.72	66.1±9.31	7.06±0.37	−0.0105	−0.265	364	<0.01
91 × 98	10.69±0.88	75.3±10.22	6.95±0.49	−0.0160	−0.334	186	<0.001
82 × 59[a]	10.63±0.82	65.6±8.37	6.62±0.34	0.0000	+0.001	165	n.s.
82 × 98 *a*	9.79±0.71	54.6±5.85	7.50±0.40	−0.0077	−0.088	28	n.s.
82 × 98 *b*	12.06±1.35	39.3±3.75	7.72±0.36	−0.0130	−0.135	173	<0.10
a and *b*	—	—	—	−0.0136	−0.241	201	<0.01
60[a] × 59[a]	9.55±1.08	58.9±7.74	7.26±0.37	+0.0058	+0.122	90	n.s.
60[a] × 62[a]	9.78±1.35	65.9±10.88	7.12±0.46	+0.0008	+0.007	56	n.s.

[a]Fish from Japan.

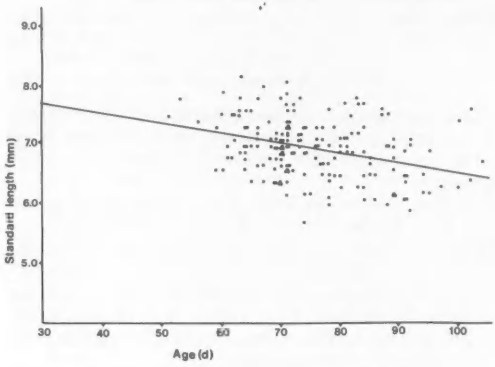

FIG. 1. Plot of SL vs. age at metamorphosis of progeny from cross 91 × 98, reared at 10.69 ± 0.88°C. Regression coefficient = −0.0160, $r = -0.334$, $P < 0.001$.

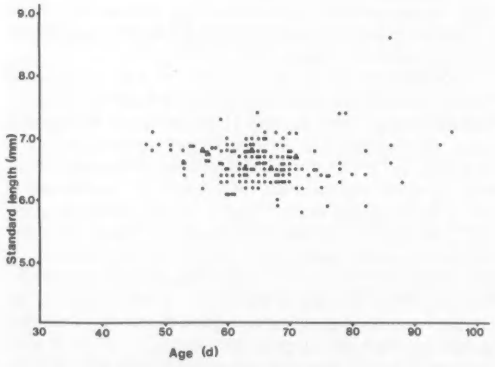

FIG. 2. Plot of SL vs. age at metamorphosis of progeny from cross 82 × 59, reared at 10.63 ± 0.82°C. Regression coefficient = 0.0000, $r = 0.001$.

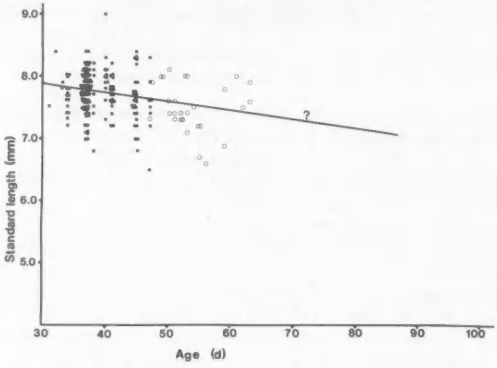

FIG. 3. Plot of SL vs. age at metamorphosis of progeny from cross 82 × 98. Closed circles represent fish reared at 12.06 ± 1.35°C; open circles represent fish reared at 9.79 ± 0.71°C. "?" represents a fish that had metamorphosed at 72 d, but was dead and therefore not measured. Regression coefficient = −0.0136, $r = -0.241$, $P < 0.01$.

Discussion — To understand the demography of fishes one must know the relationship between age and size at metamorphosis. My results suggest that although age and size both influence the onset of metamorphosis in starry flounder, the influence of size is stronger. If this relationship obtains in nature, then one would expect to find a great range in the age at metamorphosis, strongly influenced by factors such as water temperature and food supply, with relatively little variation in size. Because both mortality and dispersal are high in the pelagic stage, this would lead to reduced local recruitment in cold years, or in years with low food supply.

There has been little attention paid to the demography of metamorphosis in other fish species. In the few papers that present data on age and size at metamorphosis the authors were not primarily concerned with that interrelationship. Thus Hunter and Kimbrell (1980) reported that increased temperature decreased time to metamorphosis in the Pacific

mackerel (*Scomber japonicus*), but defined metamorphosis as the attainment of a length of 15 mm rather than the attainment of a specific developmental stage. Riley (1966) showed that poorly fed plaice (*Pleuronectes platessa*) larvae metamorphosed at a smaller size but only 4.2% later (from fertilization) than well-fed larvae. He concluded that the "onset of metamorphosis is not controlled to any large degree by size but by a mechanism dependent on temperature and time." This appears to mean that plaice metamorphosed at a wide range of sizes over a small range of ages, and that the range of ages was dependent on temperature. Unfortunately Riley did not present data on the ages and sizes of individual fish at metamorphosis, and the exact relationship between them is not obtainable from his paper, but his results do seem to be different from mine.

The demography of metamorphosis has been considered for amphibians. Smith-Gill and Berven (1979) concluded that the best predictor of metamorphosis in the frogs *Rana pipiens* and *R. sylvatica* was differentiation rate, i.e. the rate at which the next developmental stage will be reached. Differentiation rate was closely correlated with growth rate at any temperature, but temperature affected growth rates and differentiation rates differently, making growth rate a poorer predictor of metamorphosis than differentiation rate. In the present study there was no evidence that a change in temprature changed the relationship between growth rate and differentiation rate. The distribution of points shown in Fig. 3, which represents fish reared at two temperatures, is similar to that in Fig. 1, and the results of other crosses not plotted (Table 1), which represent fish reared at only one temperature. It is clear that for both frogs and flounders, age was a poor predictor of metamorphosis.

A process related demographically, and probably developmentally, to metamorphosis is sexual maturation, and this has received much attention. Demographically, sexual maturation is considered to be age dependent both in fishery texts (e.g. Everhart et al. 1975) and general texts (e.g. Futuyma 1979). But there is evidence for many organisms that the onset of sexual maturity is not age determined. It is becoming accepted that size is more important than age as a predictor of the demographic fate of plants, which share such life history parameters as indeterminate growth with fishes. For example, Werner and Caswell (1977) have shown that models based on morphological stages (size) were better predictors of first flowering, i.e. sexual maturity, in a perennial plant than were age-based models. There is also evidence that the onset of sexual maturation in fishes is either size dependent (e.g. Alm 1959; Pitt 1975; Sohn 1977) or dependent on a complicated and variable function of both age and size (e.g. Beverton 1963; Bowering 1976; Kallman and Borkoski 1978).

It appears that although no general rule can yet be established, the importance of size in mediating demographically significant stages of fishes' life histories has been underestimated. This is important, because where the onset of such stages is strongly influenced by size rather than age, as is the case of metamorphosis in the starry flounder described here, environmental variation will have a much greater effect on population processes.

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Application of Time–Series Intervention Analysis to Fish Ventilatory Response Data

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The development of environmental monitors based on ventilation behavior of fishes has produced large masses of data for which no standard analytical procedures exist. This report demonstrates the application of time–series models to this type of data. It also demonstrates the use of intervention analysis to determine the reaction to changes in water quality. Intervention analysis is a powerful statistical tool that allows for great flexibility in the type of response that can be investigated. In this report it is used to determine the ventilatory reaction of the bluegill (*Lepomis macrochirus*) to sublethal concentrations of zinc sulfate applied in fluctuating intermittent exposures.

Key words: intervention analysis, time–series models, *Lepomis*, ventilatory behavior, biomonitoring

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La mise au point de moniteurs expérimentaux fondés sur le comportement de ventilation des poissons a engendré un volume important de données pour lesquelles n'existe pas encore de méthode analytique standard. Nous démontrons dans l'article qui suit l'application de modèles de séries chronologiques à ce type de données. Nous démontrons en outre l'utilisation de l'analyse d'intervention dans la détermination de la réaction à des changements dans la qualité de l'eau. Cette analyse est un puissant outil permettant une grande flexibilité du type de réaction qui peut être étudié. Nous l'utilisons ici pour déterminer la réaction ventilatoire du crapet arlequin (*Lepomis macrochirus*) à des concentrations sublétales de sulfate de zinc appliqué dans des expositions intermittantes et changeantes.

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THE ventilatory or "breathing" rate has long been used as an indicator of stress in fishes (Belding 1929; Jones 1938; Roberts 1964; Carlson and Drummond 1978; Sorensen and Burkett 1978). However, only recent advances in the electronics and computer industries have made the continuous recording of ventilatory behavior feasible and thus have allowed the development of water quality monitors based on this response (Cairns and van der Schalie 1980).

Past analyses of ventilatory data have concentrated on the description of general trends in the response, and conventional, parametric procedures (ANOVA) have been appropriate when comparison is between individuals, and sample size is large (K.W. Thompson et al., unpublished data). Statistical comparisons between data from a single fish, stressed and unstressed, would be useful. However, problems occur in such analysis because consecutive recordings are not independent observations. A recently developed technique, applicable to such an analysis, is intervention analysis which provides a detailed description of the data as well as statistical tests of the nature and magnitude of the changes related to

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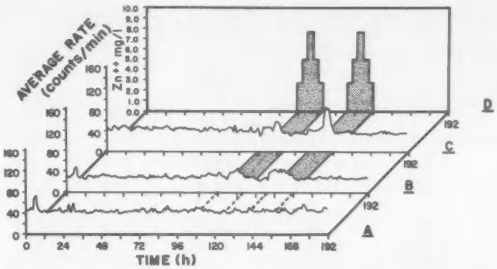

FIG. 1. Average ventilatory rates for three bluegills. (A) Control, no exposure. (B and C) Treated with zinc-sulfate solution. (D) Toxicant concentration as mg/L Zn^{++}

environmental stress (Box and Tiao 1975). Previous uses of this technique have been for analysis of long-term environmental data (Box and Tiao 1975; Hipel et al. 1978). This report demonstrates the applicability of this technique for analysis and description of the normal ventilatory response of the bluegill (*Lepomis macrochirus*), as well as the response to environmental stress caused by sublethal amounts of toxicant solutions.

Materials and methods — The minute bioelectrical signal generated by the contraction of the muscles in the pharyngeal region of a fish during gill ventilation can be detected electronically with noncontact electrodes and suitable amplifiers. These ventilatory signals can be detected, accumulated, and stored for analysis with minicomputers. This procedure, the physical system necessary to carry it out, and the computer software have been described in detail elsewhere (Thompson et al. 1978; Cairns et al. 1980; Cairns and Thompson 1980).

The ventilatory signals from three bluegills were accumulated over 15-min intervals for a period of 192 h. Two of the fish were exposed to sublethal amounts of a zinc-sulfate toxicant solution, and the third was unexposed as a control. The toxicant solution was applied for two 16-h periods — the first from hour 96 to hour 112 and the second from hour 128 to 144. The concentration of the toxicant was variable and was maintained at each level for 3 h with the exception of the maximum concentration which was maintained for 4 h. The concentration as mg/L Zn^{++} at successive levels was 2.8, 5.1, 7.8, 5.1, and 2.8 (Fig. 1). A 16-h recovery period was allowed between the successive applications.

The fish were isolated from visual and physical stimuli and held under continuous light at 22°C during the recording period. They were not fed in the recording chambers or for 24 h prior to being placed in the chambers; they were allowed to acclimate in the recording chambers for 24 h before recording began.

Statistics — The data were smoothed for analysis by summing four consecutive 15-min recordings and dividing by 60 to produce an average ventilatory rate (counts/min) for each of the 192 h. These hourly averages constitute the time series that were analyzed.

Successive toxicant exposures were initiated at the beginning of hours 96 and 128. The initial recording point was time 0; thus, the average ventilatory rate for hours 96 and 128 would be indicated as 97 and 129, and in subsequent calculations the exposure periods are indicated as 97–112 and 129–144.

A time series may consist of observations $Y(0)$, $Y(1)$, $Y(2)$, ... $Y(N)$ taken at equispaced time points. Given two time series $X(t)$ and $Y(t)$, $t = 0, \pm1, \pm2, \ldots$, it is often of interest to formulate a model of the relationship between X and Y. This can be done to describe the relationship or to estimate the magnitude and nature of the influence that X has on Y. In this context, the conventional techniques of regression analysis may be difficult to apply, because the observations are typically serially correlated, and are often cyclic (seasonal, diurnal, etc.). Hence, regression models for predicting $Y(t)$ from $X(s)$, $s = t, t-1, t-2, \ldots$, will usually be complicated, possibly involving many parameters, and will be difficult to estimate accurately. The time–series models described by Box and Jenkins (1976), however, are typically of a simple structure, are relatively easy to estimate, and have been shown to fit many real life time series with a high degree of accuracy (Box and Jenkins 1976).

Intervention analysis (Box and Tiao 1975) is an advanced type of time–series modeling that is useful for the analysis of environmental changes (Hipel et al.1978). A description of the procedures involved and some examples from environmental studies can be found in Hipel et al. (1978).

In general, a time series, Y, has been observed over a period of time, during which a change has taken place in the system or environment from which Y arose. This change, called the intervention, could be in the form of a natural or human caused perturbation of the environment. In the present study, $Y(t)$ is the average ventilatory rate given as counts/min of a fish during hour number t, and the intervention consists of the introduction of a sublethal concentration of a toxicant solution.

It is of interest to determine if the intervention has had a statistically significant effect on the process, Y. To do so, Box and Tiao (1975) suggest the following three-step strategy by which the intervention analysis is carried out, and they give the methodology necessary for each step: (1) formulate a model to describe the normal behavior of Y, along with the anticipated change in Y as a result of the intervention; (2) estimate the parameters in the model that has been formulated; and (3) perform diagnostic checks on the estimated intervention model. If not adequate, the model should be adjusted as suggested by the analysis and rerun. A computer package capable of carrying out this procedure was used to analyze the ventilatory time series from each of the three fish (Pack 1977). A chi-squared test described by Box and Jenkins (1976) was used to test for model adequacy.

All individual bluegills would not be expected to fit the same model. Individuals that fit a single model were selected for this study to illustrate the use of the procedure. The general form of the intervention is:

(1) $Y(t)$ = normal behavior + intervention effect.

The first component on the right side of the equation is that part of $Y(t)$ that is explainable by its own past (i.e. $Y(t-1)$, $Y(t-2)$, ...) and any purely random factors that cannot be accounted for. The identification of this component is carried out using preintervention ventilatory data with techniques out-

TABLE 1. Summary of the results of the time–series intervention analyses. Numbers in parentheses are standard errors of the mean.

Fish	Φ	μ	ω_1	ω_2	θ_1	θ_2
A	0.448 (0.006)	46.3 (0.514)		Control fish, no interventions		
B	0.491 (0.072)	29.4 (0.533)	0.849 (0.209)	1.590 (0.507)	7.524 (1.439)	0.470 (0.239)
C	0.720 (0.057)	43.5 (1.450)	0.745 (0.419)	1.913 (0.860)	1.750 (0.442)	1.832 (0.737)

lined by Box and Jenkins (1976). The second term in model (1) is that part of $Y(t)$ that occurs as a result of the influence of the intervention. If the intervention occurred at time t^*, then the second term on the right side of model (1) would be zero when t is less than t^*.

Results and discussion — The normal behavior of all three fish in this study was found to be best described by the following first order, autoregressive model:

$$(2)\quad Y(t) = \phi\,(Y(t-1) - \mu) + \mu + \epsilon(t).$$

The time series $Y(t)$ is the average ventilatory rate per minute during hour t. The parameter ϕ is analogous to a regression coefficient in the regression of $Y(t)$ onto $Y(t-1)$, and μ is the average ventilatory rate under normal (nonintervention) conditions. The random variables $\epsilon(t)$ are normally distributed independent variables having a mean of zero and a constant variance. The calculated values of ϕ and μ and the estimated standard errors are presented in Table 1. The test for model adequacy indicated that model (2) was an appropriate description of normal ventilatory behavior for all three fish ($\alpha = 0.05$).

To investigate the ventilatory response of the fish to the exposures to sublethal concentrations of toxicant administered as described earlier, the following intervention model was hypothesized for fish B and C:

$$(3)\quad Y(t) = \phi(Y(t-1) - \mu) + \mu + \epsilon(t) + \left[\frac{\omega_1 B^{L1}}{1-B} - \frac{\omega_2 B^{L2}}{1-B} - \frac{\omega_1 B^{L3}}{1-B} + \frac{\omega_2 B^{L3}}{1-B}\right] X_1(t) + \left[\frac{\theta_1 B^{L4}}{1-B} - \frac{\theta_2 B^{L5}}{1-B} - \frac{\theta_1 B^{L6}}{1-B} + \frac{\theta_2 B^{L6}}{1-B}\right] X_2(t).$$

The time series $X_1(t)$ and $X_2(t)$ represent the presence or absence of toxicant in the environment. During the first introduction of zinc-sulfate solution ($t = 97-112$), $X_1(t) = 1$ while for all other values of t, $X_1(t) = 0$. Similarly, $X_2(t) = 1$ for t in the interval (129–144) and $X_2(t) = 0$ for all other t. The process $X_2(t)$ indicates when the second introduction of toxicant occurred. The ventilatory responses of the fish to the toxicant exposures were found to be accurately modeled by a type of "sawtooth" pattern in which the increase in ventilatory rate was approximately linear as the toxicant concentration increased. This was followed by a similar linear decrease to near the average preexposure rate as the toxicant concentration was reduced to zero. Such a response was modeled by functions of the form:

$$\frac{\omega_1 B^{L1}}{1-B} - \frac{\omega_2 B^{L2}}{1-B} - \frac{\omega_1 B^{L3}}{1-B} + \frac{\omega_2 B^{L3}}{1-B}.$$

The parameters in this expression are interpreted as follows: B = the backshift operator, $B^L Y(t) = Y(t-L)$; ω_1 = rate change per hour in the average ventilatory rate beginning $L1$ h after the introduction of the toxicant at hour t^*; L = estimated lag time between initiation of the respective interventions and a significant change in rate (i.e. inflection points). From hours $t^* + L2$ to $t^* + L3 - 1$, the average ventilatory rate decreases by $\omega_1 - \omega_2$ counts/min. Thre is no change in the average ventilatory rate from $t^* + L3$ to $t^* + 15 + L1 - 1$. The ventilatory rate changes at an average rate of $-\omega_1$ counts/min from $t^* + 15 + L1$ to $t^* + 15 + L2 - 1$. From $t^* + 15 + L2$ to $t^* + 15 + L3 - 1$ the rate changes at an average of $\omega_2 - \omega_1$ counts/min. The average rate is at the preintervention level from $t^* + 15 + L3$ until the end of the experiment. The parameters θ_1 and θ_2 and $L4$–$L6$ in the second intervention component in (3) are interpreted in an identical fashion. The estimated values of the ω's and θ's are given in Table 1, and the inflection points (L) are summarized in Table 2.

The average ventilatory rates during periods of nonexposure were estimated to be 46.3, 29.4, and 43.6 counts/min, respectively, for fish A, B, and C. The control (A) remained at a relatively constant rate throughout the entire 192 h, while both exposed fish responded with rate increases of varying magnitude corresponding to the toxicant exposures (Fig. 1).

The intervention model hypothesized for fish B indicated a significant increase in the ventilatory rate beginning 8 h after first exposure (Fig. 1). The maximum average rate reached was 46 counts/min, an increase of ~56% with respect to the normal rate for this individual. After 9 h of increasing rates, the rate decreased for 3 h, eventually leveling off at approxi-

TABLE 2. Inflection points (L) indicating changes in the ventilatory rate of the treated individuals. Values of L are hours since the toxicant was introduced. Values in parentheses are elapsed time from $t = 0$.

Fish	$L1$	$L2$	$L3$	$L4$	$L5$	$L6$
B	8 (105)	17 (114)	20 (117)	1 (130)	9 (138)	16 (145)
C	12 (109)	13 (110)	18 (115)	11 (140)	13 (142)	19 (148)

TABLE 3. Ninety-five percent confidence limits for intervention parameters.[a]

Fish	ω_1	ω_2	θ_1	θ_2
B	0.439, 1.259	0.596, 2.580	4.704, 10 344	0.001, 0.938
C	−0.076, 1.565[b]	0.227, 3.600	0.885, 2.617	0.386, 3.277

[a]Exclusion of zero from these confidence limits indicates significant departure from normal behavior during toxicant exposure.

[b]The 90% interval for this parameter did not contain zero.

mately the preintervention rate about 35 h after the toxicant was first introduced. A second increase in the ventilatory rate was indicated beginning 1 h after the initiation of the second toxicant exposure. The rate continued to increase for 8 h, reaching a maximum average of 44 counts/min. The ventilatory rate then declined, eventually leveling off near the preexposure rate at the end of the second toxicant exposure.

The model hypothesized for fish C indicated an increase in rate beginning 12 h after first exposure to the toxicant solution. The increase continued for only 1 h and reached a maximum average rate of 61 counts/min. This was an increase of ~40% with respect to the normal average rate of 43.6 for this fish. The rate then decreased during the following 5 h and leveled off near the preintervention rate 2 h after the first toxicant exposure ceased. A large increase in rate was indicated in response to the second toxicant application for this individual. This began 11 h after the initiation of this exposure and reached a maximum average rate of 88 counts/min in 2 h. This was an increase of 126% with respect to the preexposure rate. The rate then decreased for 6 h, leveling off at approximately the normal rate 3 h after the end of the final exposure to the toxicant.

The chi-squared tests for the adequacy of the intervention model (3) indicated that the model adequately described the data at a probability level of 0.03 or less for both of the treated fish (B and C). Ninety-five percent confidence limits for the ω's and θ's are given in Table 3. The exclusion of zero from the confidence limits of the ω's and θ's, with one exception (Table 3), as well as the tests of model adequacy, are strong indications of departure from normal behavior when under the influence of toxicant solutions.

While this paper is intended primarily as a demonstration of the applicability of intervention analysis to this type of data, it is of interest to note that in three of the four interventions modeled, the ventilatory rate was decreasing before the toxicant application ceased. This could indicate acclimation to the presence of the toxicant, but is more probably a response to the reduction of the concentration of the toxicant in the final stages of toxicant application.

The exact form of the intervention part of the model in model (1) is determined by the investigator, and then adjusted if the diagnostic checks so indicate. The types of response that can be modeled are countless. One strength of this approach is that the models are typically very simple to interpret and often have very few parameters, even in describing complicated behavior. Box and Tiao (1975) discuss several models for describing various types of behavior. Another appealing feature of intervention analysis is that $Y(t)$ can be modeled as a response to any one of a number of different types of interventions, whether a one-time occurrence, a temporary change, or an intervention occurring in different forms over a long period of time.

The demonstrated usefulness of this technique for the analysis of ventilatory data should prove beneficial in the continued development of environmental quality monitoring systems based on the ventilatory response.

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An Improved Chamber for in situ Measurement of Primary Productivity by Sea Ice Algae

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A modified chamber was designed for in situ measurement of carbon uptake of microalgae growing on the underside of sea ice. The chamber, operated by SCUBA divers, accommodates a wider range of ice conditions, has better holding capability, and reduces sample loss during retrieval.

Key words: Arctic Ocean, sea ice algae, primary productivity

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Une chambre modifiée a été conçue dans le but de mesurer in situ la captation du carbone par les micro-algues croissant à la face inférieure de la glace de mer. Cette chambre, sous la direction d'un scaphandre autonome, peut accommoder une gamme plus étendue de conditions de glace, a une meilleure capacité de stabulation et diminue la perte d'échantillons au moment du prélèvement.

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THE occurrence of algae growing in sea ice is a widespread phenomenon that has been documented in both Arctic (Apollonio 1961; Meguro et al. 1967; Horner 1976) and Antarctic regions (Bunt and Wood 1963; Hoshiai 1977). Algae may occur throughout the ice, but growth is most developed during spring in a layer of unconsolidated crystals on the undersurface of the ice. This community has been termed the "epontic" community by Bunt and Wood (1963) and consists primarily of pennate diatoms and flagellates living attached to ice crystals and in brine pockets and interstitial water between crystals.

The need for a good in situ method for measuring primary productivity of the epontic community in the Arctic prompted Clasby et al. (1973) to design a combined sampler/incubation chamber that could be operated by SCUBA divers. Their chamber was constructed of 4.8-cm-diameter Plexiglas coretube lining, 4 cm in length. One end was closed off with a Plexiglas plate fitted with a rubber septum to accommodate introduction of ^{14}C-bicarbonate solution with a syringe, and the top of the sampler was serrated to cut into the ice. Following incubation, a metal spatula was used to chip away ice from around the chamber and then sever the top of the core. The sample was retained in the chamber by a core cap. This chamber was also used to collect samples for plant pigment, standing stock, nutrient, and other analyses. Although used successfully to measure primary productivity in sea ice near Point Barrow, Alaska, we felt that the chamber should be redesigned to provide for more secure attachment to the ice and to reduce sample loss that may occur during core extraction and capping.

We incorporated two new features into the chamber. One was a holder equipped with four threaded stainless steel pins adjusted to protrude ~2 cm from the chamber mouth (Fig. 1). The chamber can be hammered into the ice where the pins anchor it securely. The other new feature was a scraper with a locking pin that fit into a guide in the holder. At the end of the incubation period, while the chamber is still anchored to the ice, the pin is started into the guide, and the core severed as the scraper is pushed into place, sealing the chamber mouth. The scraper is secured by a handle on the bottom of the holder that is screwed tightly against the pin. The chamber can then be returned to the surface with little sample loss. As an added precaution when returning the chamber to the sur-

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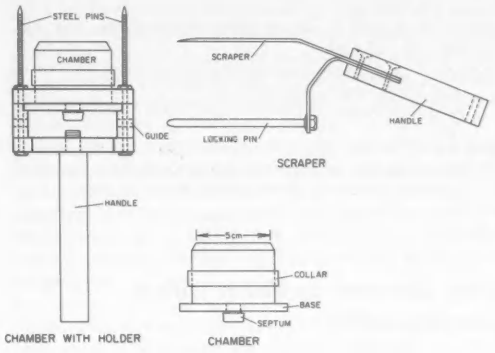

FIG. 1. Ice algal incubation chamber.

face, the scraper is held tightly over the chamber mouth to prevent leakage.

To measure dark uptake, a darkened chamber is hammered into the ice and the scraper inserted to enclose the ice sample prior to injecting the isotope. This allows the chamber to remain in place during the incubation period. As the added weight of the scraper has a tendency to pull the sampler from the ice, a doughnut-shaped float is placed over the handle to provide additional security.

The chamber is constructed of 5 cm inside diameter clear Lexan plastic tubing, 4.5 cm high, with 0.5-cm-thick walls. The upper edge is beveled and the bottom glued to a square plastic base drilled to accept a serum bottle septum. The chamber is placed in its holder by dropping the base through a square opening and rotating 45°, so that two opposite corners of the base are supported by the side supports of the holder. A tight-fitting plastic collar is slipped over the outside of the chamber to help keep it in place during handling. The base of the holder is an open H-shape to allow access to the septum for inoculation with a syringe. In practice, the chamber is rarely removed from the holder except for maintenance.

The scraper is constructed from stainless steel, with the blade tempered to increase durability. A Lexan handle is attached at a 30° angle to provide clearance for the diver's hand when scraping the flat undersurface of the ice.

The chamber was field tested in spring 1980 at a station 25 km offshore from Prudhoe Bay, Alaska. The ice was 1.7 m thick. A variety of conditions was encountered on the underside of the ice during the 2 months the station was occupied. In early April, when the algal community was beginning to develop, the unconsolidated layer was only a few millimetres thick. During the latter part of April, and throughout May when the ice algal community was most developed, the depth of the unconsolidated layer varied between 1 and 2 cm. In early June when the ice began to soften, the algae were associated with a layer of vertically oriented platelets about 1 cm thick that was easily washed from the ice by bubbles from the diver's breathing apparatus. As the ice began to melt, the algal layer dissociated from the hard ice, forming a layer several centimetres thick that was loosely associated with the ice, and eventually diffused into the water column. Following the dissociation of the ice algal layer, melt water began to refreeze into large platelets up to 40 cm in diameter and formed a zone up to 0.5 m thick.

The new chamber performed satisfactorily under the range of conditions encountered. It remained in place well and divers did not observe sample loss during extraction. The chamber was difficult to use in the layer of large platelets formed from refreezing melt water, because the platelets were easily broken or dislodged in placing the chamber. We were able to sample the firmer ice underlying this zone, but found few algal cells as the algae had dissociated from the ice by this time.

The major limitation of the chamber appears to be the thickness of the layer of unconsolidated ice. It is important that the chamber penetrate to the bottom of this layer to reduce loss of label due to diffusion. The sampler will penetrate ~4.5 cm of unconsolidated ice and is limited by the height of the chamber. By lengthening the chamber, pins, and scraper assembly, this design should work well in ice several times this depth. If the individual ice crystals are very large, such as may occur in the Antarctic (Bunt 1963), the entire chamber would need to be enlarged to minimize damage to the integrity of the ice matrix.

At intervals throughout the study, we attempted to compare rates of primary production measured by the older core-liner type chamber and the new chamber. We were unsuccessful because the core-liner type chamber would not remain in place in spite of numerous attempts by the divers. The failure of the core-liner type chamber to remain in place was probably due to the shallowness of the unconsolidated ice layer that was about 1 cm thick throughout most of the study, whereas when the core-liner type chamber was used successfully, this layer was about 2–5 cm thick.

Although we feel that our chamber offers an improvement over previous methods, several problems have yet to be overcome before we can adequately assess rates of primary production in sea ice. Because the ice algal layer is often formed of a matrix of ice crystals, it is difficult to ensure adequate mixing of the isotope throughout the sample. The addition of a stirring apparatus to the chamber may prove worthwhile, but artificial mixing would tend to destroy gradients which probably exist within the ice matrix and could affect carbon uptake rates. Also, because of the porous nature of the ice, an unknown amount of label may diffuse upward into the ice during incubation. An estimate of this loss could be obtained by determining the total amount of isotope recovered at the end of the incubation period.

An additional problem is encountered when an area is sampled repeatedly by SCUBA divers. Exhaust air from the diver's breathing apparatus collects on the bottom of the ice leaving "pockmarks" or "craters," and divers have observed a reduction in algal growth within these craters. The use of a diving apparatus that would exhaust air directly to the surface would alleviate this problem.

These experimental problems lead to an underestimation of primary production by the ice algal community. It is therefore suggested that all such reported productivity data be considered as minimum values.

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Graphical Model of Thermoregulatory Behavior by Fishes with a New Measure of Eurythermality

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The behavioral responses of fishes, specifically preference and avoidance reactions, to temperature are described using a general graphical model based on a broad overview of the literature. A quantitative measure of eurythermality, based on the area of the thermal preference zone, is presented which offers a more meaningful estimate of the optimal thermal requirements of the species than one based on lethality alone. We also emphasize the importance of considering the preference–avoidance responses of fishes when setting ambient water quality criteria for temperature or when estimating the potential environmental impact resulting from changes in the thermal regime of an aquatic system.

Key words: thermoregulation, behavior, temperature, eurythermality, thermal preference, avoidance

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Un modèle graphique général fondé sur un survol des travaux publiés sert à décrire les réponses éthologiques des poissons, particulièrement les réactions de préférence et d'évitement de la température. Nous donnons une mesure quantitative de l'eurythermalité, fondée sur la superficie de la zone de préférence thermique. Cette mesure conduit à une meilleure estimation des exigences thermiques optimales de l'espèce qu'une estimation fondée sur la létalité seule. Nous faisons en outre ressortir l'importance de tenir compte des réponses de préférence–évitement des poissons en établissant les critères de qualité de l'eau ambiante quand à la température ou en estimant l'impact environnemental qui pourrait résulter de changements dans le régime thermique d'un système aquatique.

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FOUR general hypotheses have emerged as unifying concepts in the study of behavioral thermoregulation by fishes: (1) the final temperature preferendum is a species-specific response to a temperature gradient, but can be modified by nonthermal acclimatization factors, such as age, food availability, season, or pathologic condition (e.g. Sullivan and Fisher 1953; McCauley and Read 1973; Peterson 1973, 1976; Reynolds and Casterlin 1976, 1978a, 1980; Reynolds et al. 1976; McCauley 1977); (2) habitat partitioning by thermoregulatory behavior is one means of segregating fishes both intra- and inter-specifically, thereby reducing cannibalism and competition (e.g. Reynolds and Casterlin 1978b; Brandt et al. 1980; Coutant 1980; Crowder et al. 1981); (3) preferred temperatures may reflect thermal optima for certain biological processes (e.g. Crawshaw 1977; Magnuson et al. 1979; Coutant 1980); and (4) fishes generally avoid thermal extremes before they become lethal, provided favorable temperatures (thermal refugia) are available (e.g. Cherry et al.

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1975, 1977; Gift 1977; Winkler 1979). The *sine qua non* of each hypothesis is the ability of fishes to perceive and to respond to temperature changes in an adaptive manner. After we conducted a broad review of the literature, it became apparent that the behavioral responses of fishes (preference and avoidance) to temperature could be summarized with a general graphical model which provides a conceptual framework for understanding the more elusive effects temperature has on the movements of many fish species. The purpose of this paper is to present this model with supporting data from the literature, and to define (using the model) a quantitative measure of eurythermality based on behavioral responses to temperature.

Definition of terms — A variety of laboratory methods have been used to determine the thermal responses of fishes (McCauley 1977). In general, regardless of the methods used, laboratory studies have demonstrated the abilities of fishes to thermoregulate behaviorally within relatively narrow limits. A measure of the central tendency (mean, mode, median, or midpoint) of the frequency distribution of a fish species within a laboratory thermal gradient over a short period of time (2 h or less) is termed the *acute preferred* or *acute thermal preferendum* (Reynolds and Casterlin 1979a), which is highly dependent on acclimation temperature (see Mathur and Silver (1980) for discussion of statistical problems associated with acute temperature preference studies). The *final temperature preferendum*, on the other hand, is the temperature around which fish finally will congregate given the opportunity to do so in a thermal gradient of sufficient extent (Fry 1947). This value is independent of acclimation temperature and can either be measured directly over a period of 1−4 d (Richards et al. 1977), or estimated as the temperature at which the preferred temperature equals the acclimation temperature. When placed in a gradient, fish acclimated to temperatures below their final preferendum will generally move into higher temperatures (acute thermal preference), resulting in a progressive and relatively rapid increase in acclimation temperature for the fish. This upward trend in temperature preference occurs until the final preferendum is attained, and the fish continues to thermoregulate around this temperature. If the gradient is spatially shifted, fish will move with the gradient so that body temperatures are maintained within narrow limits ("isotherm-tracking" (Reynolds and Thomson 1974; McCauley et al. 1977)).

Avoidance responses of fishes to temperature also have been determined using a variety of techniques. Generally, avoidance can be measured directly by providing fish with a choice between water which is heated or cooled and water at the acclimation temperature of the fish (e.g. Meldrim and Gift 1971 and Cherry et al. 1975, 1977, as modified from Shelford and Allee 1913). The avoidance threshold, then, is defined as the temperature at which fish spend significantly less time in comparison to controls. Avoidance can also be estimated indirectly by determining the median upper and lower turnaround temperatures using an electronic shuttlebox (Neill et al. 1972; Neill and Magnuson 1974); turnaround temperatures are defined as the local temperature maxima and local temperature minima recorded from the warmer and cooler sides of the tank, respectively (Neill and Magnuson 1974).

Although the words "selection" and "preference" have been used synonymously in the literature, "selection" might be mistaken for "natural selection" as an evolutionary process. For this reason, we prefer the term temperature preference in the organismic context.

Model of thermoregulatory behavior — Temperature preference and temperature avoidance are simply opposite sides of the same coin (Reynolds 1977); these responses are inseparable aspects of behavioral thermoregulation under natural conditions. Given this, it is not surprising to find that both preference and avoidance behavior are altered by a variety of environmental, as well as anthropogenic, factors. Preference−avoidance responses to temperature can vary on a diel and/or seasonal basis which may reflect changing thermal requirements for a species over time (Sullivan and Fisher 1953; McCormick et al. 1977; Reynolds and Casterlin 1979b, 1980). Also, changes in water quality, light intensity, food availability, competition, bacterial infections, and age can alter the thermoregulatory behavior of any given species under laboratory conditions (Sullivan and Fisher 1954; Ferguson 1958; Ogilvie and Anderson 1965; Covert and Reynolds 1977; Reynolds et al. 1977; Coutant 1980). Despite the many complicating factors that are possible, comprehensive field investigations have shown that temperature is extremely important in determining the distribution patterns of many species, and these patterns can be predicted on the basis of temperature preferenda of the individual species (Neill and Magnuson 1974; Stauffer et al. 1976; Coutant 1980). In addition, avoidance responses under field conditions have been documented by many authors for a variety of species (e.g. McCauley and Tait 1970; Marcy et al. 1971; Cherry et al. 1976; Ehrlich et al. 1978; Winkler 1979). Overwhelming evidence, therefore, supports the general conclusion that the preference−avoidance response to temperature is an ecologically significant behavior that influences the distributions and movements of fishes. Variability of this behavior under different sets of conditions is not unusual, considering that habitat selection is based on the optimization of various environmental factors which fit the particular morphological, physiological, and behavioral characteristics of a species. Thus, the relative influence of each environmental factor on thermoregulatory behavior in a natural ecosystem will most likely change depending upon the biological "needs" of an organism at a particular time.

Before any reliable recommendations can be made concerning appropriate water quality criteria for temperature, and before reliable estimates of the potential impact of thermal discharges on aquatic resources can be made, behavioral responses of indigenous species must be considered (Hoss et al. 1979). The behavioral model we propose offers a general means of viewing the sublethal effects of temperature on locomotor behavior in relation to lethal effects (Fig. 1). This model is patterned after the classical temperature tolerance polygon described by Fry (1947) and Brett (1956), and was suggested from data presented by Reynolds and Casterlin (1979a) on the thermal relations of bluegill sunfish (*Lepomis macrochirus*). The thermal tolerance polygon was based on the incipient lethal temperature, defined as that temperature beyond which 50% of the population could no longer live given an indefinite period of time (Fry 1947). Fishes, however, are more sensitive to thermal changes than direct lethal

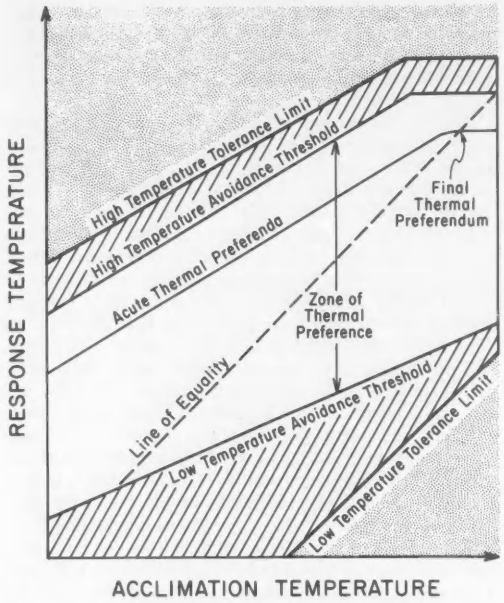

FIG. 1. Generalized graphical model which demonstrates the relationships between preferred, avoided, and lethal temperatures. Broken line (line of equality) represents points at which preferred temperature equals acclimation temperature, and is often used in estimating the final thermal preferendum.

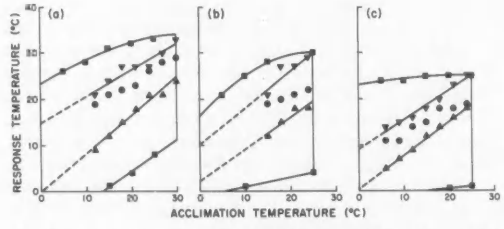

FIG. 2. Acute thermal preferenda (●), upper (▼) and lower (▲) avoidance temperatures, and lethal temperatures (■) for (a) bluntnose minnow (*Pimephales notatus*), (b) yellow perch (*Perca flavescens*), and (c) brook trout (*Salvelinus fontinalis*). Lethal temperatures were reported by Brett (1956); avoidance and acute thermal preferenda were reported by Cherry et al. (1975, 1977).

effects generally indicate. Given the choice, many species will avoid temperatures below the incipient lethal level; therefore, based on the previous discussion, it is apparent that a more detailed conceptual framework is needed to assess fish responses to temperature changes. This framework is provided in Fig. 1. The avoidance temperatures are within the range of nonlethal temperatures and bound an area referred to as the zone of thermal preference. Within this area, the acute thermal preferenda and the final thermal preferendum are distributed asymmetrically, falling closer to the upper zone of lethality. This reflects the observation that many fish prefer, without apparent harmful effects, temperatures only a few degrees below those that are lethal. The data reported for a variety of fish species are consistent with this graphical model (Fig. 2; see also Reynolds and Casterlin 1979a, 1980).

By measuring the area within the temperature tolerance polygon, Brett (1956) gave a numerical estimate (expressed as $°C^2$) of the range of thermal conditions an organism could withstand. Perhaps a better quantitative estimate of the optimal thermal requirements of an organism, however, is provided by the area within the temperature preference zone. This would also represent a more realistic quantitative measure of the qualitative terms "eurythermal" and "stenothermal," as suggested by Cherry et al. (1975). For example, the zones of tolerance for bluntnose minnow (*Pimephales notatus*), yellow perch (*Perca flavescens*), and brook trout (*Salvelinus fontinalis*) were calculated to cover areas of 808, 742, and $625°C^2$ (thermal tolerance units), respectively (Brett 1956). The zones of thermal preference for each species, however, are considerably more limited, covering areas of 338, 239, and $186°C^2$ (thermal preference units), respectively. The importance of this zone of thermal preference lies in the third hypothesis presented above, i.e. preferred temperatures may reflect thermal optima for certain biological processes. Fishes, because of their species-specific temperature preferences, segregate along thermal gradients (thermal partitioning: Reynolds and Casterlin 1978b; Brandt et al. 1980; Coutant 1980; Crowder et al. 1981). Given this, one logical assumption would be that biological processes, although capable of functioning over the range of normal habitat temperatures for a species, would function best at or near the temperature preferred by that species (e.g. Crawshaw 1977; Magnuson et al. 1979; Coutant 1980). If, then, fishes actively select temperatures that are optimum for meeting their biological needs at a particular time (certainly some evidence indicates that they do), then the zone of thermal preference, as presented in our model, may be a more accurate representation of the thermal regime a species will inhabit.

Thus, because of behavioral effects, the sublethal environmental impacts of temperature on fish communities are more subtle, but potentially as drastic as direct lethality. For example, under late fall or early spring conditions, assuming an acclimation temperature of about 10°C, brook trout prefer temperatures within the avoidance limits of 7–16°C (Fig. 2). According to our model, a water temperature greater than 16°C would have caused brook trout to avoid the area of thermal impact, even though they could have tolerated temperatures up to 24°C for some period of time.

Temperature changes could be caused by industrial thermal inputs or by unnatural heating of an aquatic system due to deforestation, impoundment, or other changes in the watershed. These changes may be undesirable in that they reduce the area of the stream having temperatures within the zone of thermal preference, and thus reduce desirable habitat for fish species. Thus, one factor affecting the severity of any thermal impact on a fish community is the area or volume of the aquatic environment affected. If the undesirable temperature effectively blocked migratory routes of passage (in lotic systems), or rendered large areas of the habitat unavailable for reproduction or feeding (in lentic systems), then the potential loss to a species would be greater than that estimated on the basis of lethality alone. Conversely, if the area of impact

were relatively small, with suitable areas of refuge or routes of passage left open, then the thermal impact would be minimal for many fish species. The potential impact of any thermal change, therefore, will be governed to a great extent by the site-specific physical characteristics of the aquatic system affected.

The graphical model we present (Fig. 1) provides a general scheme for understanding the sublethal effects temperature has on the movements of many fish species, and a more meaningful interpretation of eurythermality. Of primary importance, however, is the additional understanding gained from considering behavioral effects. By doing this, environmental scientists and managers will have a broader perspective for predicting the consequences of thermal changes in aquatic systems.

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Comment on Multivariate Analysis as a Means of Comparing Growth in Fish

Multivariate statistical methods are appropriate for analysis of many problems commonly encountered by fisheries scientists. Bernard (1981) provides a well-written explanation of Hotelling's T^2 (a multivariate generalization of the t-test), as well as an example of how to apply it to a common fisheries problem. However, we feel that several potentially misleading details of his equations should be clarified if the technique is to be applied to other problems. We also suggest a statistically more powerful method for computing confidence intervals.

Bernard's equations 5 and 7 for calculation of critical values of T_0^2 and F_0 are correct for his specific example, but can be generally stated as:

$$(5)\quad T_0^2 = \frac{C(N_1 + N_2 - 2)}{N_1 + N_2 - C - 1}\, F\alpha;\, N_1 + N_2 - C - 1$$

$$(7)\quad F_0 = \frac{N_1N_2(N_1 + N_2 - C - 1)(p_{1_j} - p_{2_j})^2}{C(N_1 + N_2)(N_1 + N_2 - 2)s_{jj}}$$

where C is the number of characteristics examined ($C = 3$ in Bernard's example). There was an erratum in equation 6 for computing Roy–Bose simultaneous confidence intervals. The variance term (s_{jj}) was omitted; the equation should be written:

$$(6)\quad (p_{1_j} - p_{2_j}) \pm \sqrt{\frac{N_1 + N_2}{N_1N_2}\, s_{jj}T_0^2}$$

The Roy–Bose procedure is appropriate for calculating confidence intervals for all linear combinations of the characteristics examined. However, this procedure provides confidence intervals that are too wide for a chosen α when the number of comparisons of interest is small in respect to all possible combinations. Bonferroni inequalities provide smaller, more precise, confidence intervals in this case (Srivastava and Carter 1982). Bonferroni inequalities should be used instead of the Roy–Bose procedure if:

$$t_0 \leq T_0$$

where $t_0 = t_{\alpha/2k;\ N_1 + N_2 - 2}$ and k is the number of comparisons of interest ($k = 3$ for Bernard's example). For Bernard's numerical example (his Table 2), Bonferroni inequalities are appropriate because:

$$t_0 = t_{0.0016;\ 154} = 2.99 < 3.45 = \sqrt{T^2_{0.01;\ 3,152}} = T_0.$$

The general formula for confidence intervals based on Bonferroni inequalities is

$$(p_{1_j} - p_{2_j}) \pm t_0\sqrt{\frac{N_1 + N_2}{N_1N_2}\, s_{jj}}.$$

The 99% confidence intervals produced by Bonferroni inequalities with Bernard's data were not much smaller than those from Roy–Bose procedure, but they did allow for rejection of the null hypothesis (H_0): $t_0(\delta) - t_0(\varphi) = 0$ in his first example. The Bonferroni confidence interval for that comparison is calculated as:

$$(p_{13} - p_{23}) \pm t_0\sqrt{\frac{N_1 + N_2}{N_1N_2}\, s_{33}}$$

$$= (-3.36) - (-4.57) \pm 2.99\sqrt{\frac{78 + 78}{(78)(78)}\, 4.9955}$$

$$= 1.21 \pm 1.07:$$

$$0.14 \leq t_0(\delta) - t_0(\varphi) \leq 2.28.$$

Because the 99% confidence interval does not include 0, we would conclude that we must reject H_0 at $\alpha = 0.01$. A greater difference in width of confidence intervals occurs with small sample sizes and larger numbers of measured characteristics.

In many cases, calculation of accurate confidence intervals requires good estimates of $F\alpha$ and $t\alpha$. If calculators or computer programs are not available, close approximations of $F\alpha$ and $t\alpha$ may be obtained by interpolation, when $F\alpha$ is bracketed by tabled values $F\alpha_0$ and $F\alpha_1$ via the formula:

$$\log\alpha = \log\alpha_0 + \frac{F\alpha - F\alpha_0}{F\alpha_1 - F\alpha_0}\,(\log\alpha - \log\alpha_0)$$

where $F\alpha_0 < F\alpha < F\alpha_1$ (Mardia and Zemroch 1978). Solving the formula for $F\alpha$:

$$F\alpha = F\alpha_0 + \frac{(\log\alpha - \log\alpha_0)(F\alpha_1 - F\alpha_0)}{(\log\alpha_1 - \log\alpha_0)}.$$

Values of $t\alpha$ may be determined as follows:

two-tailed $t\alpha$; $d = \sqrt{F\alpha;\ 1,\ d}$, and

one-tailed $t\alpha$; d = two-tailed $t\alpha/2$; d

where d is the degrees of freedom (for the two-sample case: $d = N_1 + N_2 - 2$).

We strongly recommend the soon to be published text by Srivastava and Carter for fisheries scientists interested in the use of multivariate statistical methods. The text is well

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written with many examples from natural sciences including some from fisheries. Practical applications are stressed, and theoretical details are held to a minimum. The book should be easily understood by anyone with reasonably good preparation in elementary univariate statistics — MICHAEL R. HEADRICK AND F. JOSEPH MARGRAF JR., *Ohio Cooperative Fishery Research Unit, The Ohio State University, 1735 Neil Avenue, Columbus, OH 43221, USA.*

BERNARD, D. R. 1981. Multivariate analysis as a means of comparing growth in fish. Can. J. Fish. Aquat Sci. 38: 233–236.

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EDITOR'S NOTE: *Dr D. R. Bernard has considered this Comment and agrees with the authors' points.*

Books received/Livres reçus[1]

October–November/octobre–novembre 1981

Coastal Upwelling: coastal and estuarine sciences 1. *Edited by Francis A. Richards. American Geophysical Union, Washington, D.C. 1981. xiii + 529 p.* Includes many of the contributions to the IDOE (International Decade of Ocean Exploration) International Symposium on Coastal Upwelling held in February 1980. [R384]

Author–Subject Index to Fisheries and Marine Service Translation Series: Translation Series Nos. 3001–4000. *Compiled and edited by Garry I. McT. Cowan and Judith A. Cowan. Marine Sciences Research Laboratory Technical Report No. 21, Memorial University of Newfoundland. 1981. $5.00.* The Author–Subject Index to FRB (Fisheries Research Board) Translations Nos. 1–1600 and 1601–3000 are also available for a cost of $5.00 each. Copies of the actual translations are available at a modest service charge from CISTI. [R385]

Aquatic Ecosystems: an operational approach. *Jan. E. Beyer. University of Washington Press, Seattle and London. 1981. ix + 317 p. $20.00.* A revision of Beyer's doctoral dissertation for the Technical University of Denmark in 1976. He looks at mathematical models of ecological systems in which problems arise in connection with man-made influences at both ends of the aquatic food chain: waste water discharge and fishing. [R386]

[1]Persons interested in reviewing books in this list should contact the Book Review Editor, Canadian Journal of Fisheries and Aquatic Sciences, Scientific Information and Publications Branch, Department of Fisheries and Oceans, Ottawa, Canada K1A 0E6.

[1]Les personnes intéressées à examiner les livres énumérés dans cette liste sont priées de communiquer avec le Rédacteur des comptes rendus, Journal canadien des sciences halieutiques et aquatiques, Direction de l'information et des publications scientifiques, Ottawa, Canada K1A 0E6.

Marine Invertebrates: laboratory animal management. *National Research Council (U.S.). Committee on Marine Invertebrates. National Academy Press, Washington, D.C. 1981. x + 382 p.* This manual summarizes contemporary methods for maintaining and rearing marine invertebrates in laboratories without immediate access to the sea. [R387]

Fishes in North American Deserts. *Edited by Robert J. Naissan and David L. Soltz. John Wiley & Sons, New York. 1981. x + 552 p. $42.50 (U.S.).* From a symposium sponsored by the American Society of Ichthyologists and Herpetologists, 1980. A detailed overview of the biology, history, and habitats of desert fishes with insight into the special management and conservation problems associated with the aquatic resources of North American deserts. [R388]

Study of the Sea: the development of marine research under the auspices of the International Council for the Exploration of the Sea. *Edited by E. M. Thomasson. Fishing News Books Ltd., Farnham, Surrey, England. 1981. £25.00 + £2.50 postage and packing. xivt 256 p.* A unique survey of some of the most important activities in marine oceanographic and fisheries science pursued under the ICES umbrella. Forty papers, together with the editor's explanatory notes, clearly illustrate the magnitude and complexity of the problem. [R389]

Marine Fisheries Ecosystem: its quantitative evaluation and management. *Taivo Laevastu and Herbert A. Larkins. Fishing News Books Ltd., Farnham, Surrey, England. 1981. xiv + 162 p. £15.50 + £1.55 postage and packing.* A summary of experiences and results of ecosystem simulation in the Northwest and Alaska Fisheries Center in Seattle, gained during the last 4 years. [R390]

ANNOUNCEMENTS/AVIS

Symposium on Utilization of Coastal Ecosystems

Duke University Marine Laboratory and the Fundação Universidade do Rio Grande are organizing an international symposium on "Utilization of Coastal Ecosystems: Planning, Pollution and Productivity," to be held November 22–27, 1982, in Rio Grande, Rio Grande do Sul, Brazil. This symposium expects to gather and synthesize recent information on the effects of industrial and urban growth, and exploitation of natural resources and aquaculture in estuaries, coastal lagoons, and the continental shelf, to facilitate effective management of these environments. Official languages of the symposium are English, Portuguese, and Spanish. The Brazilian National Council on the Development of Research and Technology (CNPq), and the UNESCO regional office and projects are the principle sponsors. Dr John D. Costlow (Duke University) is the president of the symposium.

For further information, please contact *the Secretary General, Dr Labbish Ning Chao, Local Committee of the International Symposium, Universidade do Rio Grande, Caixa Postal 474, 96200 Rio Grande, RS, Brazil. Telephone No. (0536) 2-20-91 Ext. 177.*

Colloque sur l'Utilisation des écosystèmes côtiers

Le laboratoire maritime de l'Université Duke et la Fundação Universidade do Rio Grande organisent un colloque international sur l'« Utilisation des écosystèmes côtiers : planification, pollution et productivité », qui se tiendra du 22 au 27 novembre 1982 à Rio Grande (Rio Grande do Sul), au Brésil. On s'attend à recueillir ainsi et à synthétiser l'information récente sur les effets de la croissance industrielle et urbaine, et sur l'exploitation des ressources naturelles et l'aquiculture en estuaires, lagunes côtières et plateau continental, afin de faciliter une gestion efficace de ces environnements. Les langues officielles du colloque sont l'anglais, le portugais et l'espagnol. Le *Brazilian National Council on the Development of Research and Technology (CNPq)* et le bureau régional de l'UNESCO en sont les principaux animateurs. Le président du colloque est le D[r] John D. Costlow (Université Duke).

Pour plus de renseignements, on est prié de communiquer avec le Secrétaire général, le *D[r] Labbish Ning Chao, Local Committee of the International Symposium, Universidade do Rio Grande, Caixa Postal 474, 96200 Rio Grande, RS, Brésil. N° de téléphone: (0536) 2-20-91 poste 177.*

Scholarly Communication Around the World: A Joint International Conference

This conference, to be held May 15–20, 1983, in Philadelphia, Pennsylvania, is sponsored by the Council of Biology Editors, the International Federation of Scientific Editors' Association, and the Society for Scholarly Publishing. The proceedings will be published.

Contributed papers (deadline for abstract May 1, 1982), discussion-group activities, and poster sessions (deadline for title March 1, 1982) are planned. The official language of the conference will be English.

The conference theme of scholarly communication around the world will be of interest to authors, editors, publishers, librarians, printers, computer scientists, users, et al.

For further information, please contact *1983 International Conference, Attention: Elizabeth M. Zipf, Biosciences Information Service, 2100 Arch Street, Philadelphia, PA 19103, USA.*

Conférence internationale sur la communication érudite dans le monde

La conférence, qui se tiendra du 15 au 20 mai 1983, à Philadelphie (Pennsylvanie), est parrainée par le *Council of Biology Editors*, la Fédération internationale des Associations d'éditeurs d'ouvrages scientifiques et la *Society for Scholarly Publishing*. Les débats en seront publiés.

Il est prévu de solliciter la rédaction de documents de travail (date limite pour le résumé : 1[er] mai 1982), et d'organiser des groupes de discussion ainsi que des séances d'affichage (date limite pour le titre: 1[er] mars 1982). La langue officielle de la conférence sera l'anglais.

Le thème de la conférence, la communication érudite dans le monde intéresse les auteurs, les rédacteurs, les éditeurs, les bibliothécaires, les imprimeurs, les informaticiens, les lecteurs, etc.

Pour de plus amples renseignements, veuillez communiquer avec *1983 International Conference, À l'attention de : Elisabeth M. Zipf, Biosciences Information Service, 2100 Arch Street, Philadelphia, PA 19103, USA.*

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Pattern identification in the microstructure of sockeye salmon (*Oncorhynchus nerka*) otoliths
S. L. Marshall and S. S. Parker

Temperature preference and avoidance responses of the crayfish, *Orconectes obscurus*, and associated statistical problems **D. Mathur, R. M. Schutsky, and E. J. Purdy Jr.**

Use of adenylate concentrations and adenylate energy charge as indicators of hypoxic stress in estuarine fish **R. D. Vetter and R. E. Hodson**

Statistical determination of data requirements for assessment of lake restoration programs
N. M. Trautmann, C. E. McCulloch, and R. T. Oglesby

Respiratory metabolism and swimming performance of the squid, *Loligo opalescens*
R. K. O'Dor

Comparisons of witch flounder (*Glyptocephalus cynoglossus*) stocks of the Newfoundland–Labrador area, based upon a new multivariate analysis method for meristic characters
W. R. Bowering and R. K. Misra

Early trend determination of orgonochlorine contamination from residue ratios in the sea lamprey (*Petromyzon marinus*) and its lake whitefish (*Coregonus clupeaformis*) host
K. L. E. Kaiser

Decline of lake herring (*Coregonus artedii*) in Lake Superior: an analysis of the Wisconsin herring fishery, 1936–78 **J. H. Selgeby**

Growth model of *Daphnia* **J. E. Paloheimo, S. J. Crabtree, and W. D. Taylor**

Paleolimnological evidence of early eutrophication in Lake Erie
G. P. Harris and R. A. Vollenweider

Seaward movement of coho salmon (*Oncorhynchus kisutch*) fry in Carnation Creek, an unstable coastal stream in British Columbia
G. F. Hartman, B. C. Andersen, and J. C. Scrivener

Stock identification of sockeye salmon (*Oncorhynchus nerka*) with scale pattern recognition
R. C. Cook

Notes

Hormone-induced ovulation of coho salmon (*Oncorhynchus kisutch*) held in seawater and freshwater **S. A. Sower, C. B. Schreck, and E. M. Donaldson**

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W. Shaul and L. Goodwin

Some estimates of population density and feeding habits of the rock crab, *Cancer irroratus*, in a kelp bed in Nova Scotia
N. C. Drummond-Davis, K. H. Mann, and R. A. Pottle

Ammonia excretion in *Corophium volutator*: using an automated method
C. M. Hawkins and P. D. Keizer

Methemoglobin levels in channel catfish, *Ictalurus punctatus*, exposed to nitrite and tricaine methanesulfonate **D. W. Huey and T. L. Beitinger**

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- **Ethics in Research**
  Ruth Macklin, *Department of Community Health, Albert Einstein College of Medicine*
- **Cheating in Science and Publishing**
  Lawrence K. Altman, *Science News Department, The New York Times*
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